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Created in 1849, the Department of the Interior—America's Department of Natural Resources—is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

As the Nation's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States—now and in the future.

REARING TILAPIA FOR TUNA BAIT

By Thomas S. Hida, *Fishery Research Biologist*, Joseph R. Harada, *Fishery Aid*, and Joseph E. King, *Fishery Research Biologist*

Bureau of Commercial Fisheries

The pole-and-line live-bait fishery for skipjack (*Katsuwonus pelamis*) is the most important commercial fishery in the Hawaiian Islands. In 1959, the catch amounted to 12.4 million pounds, worth $1.5 million to the fishermen. Brock and Takata (1955) and Yamashita (1958) stated that a critical factor limiting this fishery is the shortage of live bait during the fishing season, which extends generally from May to October and usually reaches its peak in August. Yamashita (1958) has estimated that the Hawaiian live-bait fishery utilizes about 36,000 buckets (252,000 pounds) of bait annually. Much more than this amount could be used to advantage in most years, if it were available.

The principal bait fish is the nehu (*Stolephorus purpureus*), a small anchovy. The iao (*Pranesus insularum*), a silverside, is also used in some quantity. The nehu is a delicate fish that, even if handled carefully, will not survive in the bait wells of the sampans (fishing vessels) for more than a few days. It has not been considered feasible to attempt to rear the nehu artificially.

As one approach to solving the bait-fish problem, artificial baits of both edible and inedible materials have been tested with generally negative or inconclusive results (Tester et al., 1954).

In another approach to the problem, the staff of the Bureau of Commercial Fisheries Biological Laboratory at Honolulu, Hawaii, in recent years introduced a sardine (*Harengula vittata*) from the Marquesas Islands (Murphy, 1960) and the threadfin shad (*Dorosoma petenense*) from the United States. The introductions appear to be successful, but it is too early to predict if these fishes will become abundant enough to satisfy the needs of the fishery for additional bait supplies.

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A small stock of *Tilapia mossambica* was brought to Hawaii from Singapore in 1951 by the Hawaii Division of Fish and Game. The species is now well-established in ponds and reservoirs on all major islands of the Hawaiian group. The use of tilapia as skipjack bait was first tested by Brock and Takata (1955), who reported that tilapia were used to catch fish from schools that had been first chummed to the stern of the boat with nehu. King and Wilson (1957) further demonstrated that small tilapia had many characteristics of a good bait fish and judged it to be an adequate skipjack bait. They found tilapia to be a very hardy fish that tolerated a wide range of salinities and survived for indefinite periods in the bait wells of the sampans. It was their opinion, however, that large quantities of bait-size tilapia could not be produced effectively in reservoirs and natural ponds because of the difficulty of harvesting the young fish and because of the lack of control over cannibalism and predation.

In December 1957, a contract was signed with Maui Fisheries and Marine Products, Ltd., the Territorial Board of Agriculture and Forestry, and the Bureau of Commercial Fisheries, as principals, for operation of a hatchery at Paia, Maui, to determine the economic feasibility of producing young tilapia in a system of concrete tanks. Under the terms of the contract, Maui Fisheries was to bear the cost of land rental, the major capital improvements, and the water used; the Territory was to aid in fencing the area and provide other facilities and services; the Bureau of Commercial Fisheries agreed to provide a biologist to supervise operation of the plant, to furnish feed for the fish, and to supply miscellaneous equipment such as dipnets, screens, fish-sorting devices, and chemical supplies. While not parties to the formal contract, Hawaiian Tuna Packers, Ltd., and Hawaiian Commercial and Sugar Co., Inc., expressed

their interest in the project and willingness to cooperate. In February 1959, the same organizations signed another contract with almost identical conditions, except that the Bureau of Commercial Fisheries was to bear the additional cost of the water and electricity used in the plant.

A former horse and mule stable at Paia was selected for use as a tilapia hatchery and its reconditioning and conversion began early in December 1957, and was completed in all major respects in January 1958. A biologist was stationed at the hatchery from January through December, 1958, and from February through December, 1959.

This report describes the results obtained at the Paia hatchery during the 2 years of its operation. It is hoped that this review of the problems encountered, the methods employed, and the economic aspects of the operation will prove of value and interest to fishery scientists and to members of the tuna industries who are concerned with the problem of obtaining an adequate supply of live bait.

The production of bait-size tilapia under natural conditions in two types of ponds, located in the Honolulu area, is described in the appendix. In a brackish-water pond where many natural predators were present, production and survival of young fish were essentially zero. In a freshwater pond with few predators but prevalent cannibalism, bait-size fish were produced in limited quantities.

The interesting breeding habits of *T. mossambica* have been well described by Chen (1953) and other investigators. The adult male in breeding condition establishes a territory in which he digs a saucer-shaped depression, if the bottom is of sand or mud, or clears a circular area of algae, stones, or detritus, if the bottom is of hard clay or rock. He then maintains constant vigil over his "nest," chases away any other males that approach too closely, and attempts to herd females into the nest area. If a female can be encouraged to spawn, the eggs are extruded over the nest, fertilized by the male, and are immediately taken into the mouth by the female. The female then moves away or is chased away by the male. The male remains to guard the nest and to court other females. The eggs hatch in about 60 hours, but the female continues to carry the young in her mouth cavity for another 5 to 8 days. When the young are finally released by the female they form a tight little school near the surface of the water where they are easily dipnetted. If not dipnetted during their first day of freedom they sink to the bottom or middle layers of the tank where they are more difficult to capture.

FIGURE 1.—Former stable at Paia, Maui, before being remodeled for use as a tilapia-rearing plant.

THE PAIA HATCHERY

DESCRIPTION OF FACILITIES

Tanks

The hatchery was situated near the sugar mill at Paia, Maui. The portion of the stable that was renovated consisted initially of a long, concrete-walled walkway with a narrow trough along each wall. On the outer side of each trough was a series of 45 individual stalls (fig. 1). To convert these structures into a tilapia-producing plant, the central walkway was walled at each end and partitioned in the middle to create two large brood tanks, A and B. The two narrow troughs and the 90 stalls were converted into fry tanks (fig. 2). Inflow pipes and drains were installed in all tanks. The dimensions of the various tanks are given in table 1.

A small building was moved onto the grounds and modified for storage of feed and equipment.

TABLE 1.—*Dimensions and capacities of fish tanks at the Paia hatchery*

Item	Type of tank			Total
	Brood	Fry trough	Fry	
Number of tanks	2	4	90	
Dimensions of tanks (ft.):				
Length	161	161	11	
Width	5.23	1.8	6.5	
Overall depth	2.25	1.58	1.08	
Depth of water (ft.)	2.0	1.33	1.0	
Capacity per tank:				
Cubic feet	1,684	385	71.5	2,140.5
Gallons	12,596	2,880	535	16,011
Surface area (sq. ft.):				
Per tank	84	290	71.5	
All tanks	1,684	1,160	6,435	9,279

FIGURE 2.—Stable area at Paia, Maui, after being remodeled into a system of 2 brood tanks and 90 fry tanks for rearing tilapia.

Water Supply

The water used at the Paia plant came from wells located in the same general area. It was pumped to a storage tank at a higher elevation and returned by gravity flow to the tilapia plant, arriving there under considerable pressure. Analyses showed a salt content ranging from 60 to 80 grains per gallon. The water was suitable for irrigation but was not approved for human consumption. The brood tanks, as well as the fry tanks, had an independent water supply, and none of the water was recirculated in 1958. Early in 1959, a pump and sand filter box were installed and the water in brood-tank A was filtered and recirculated during the balance of the year.

The total amount of water used was 9,285,890 gallons in 1958 and 13,100,000 gallons in 1959. The amounts used and cost by months are given in tables 2 and 3 for the 2 years. The amounts used were greater in 1959 than in 1958 because (1) of the addition of 3 holding tanks, (2) a supply of bait-size fish was held over from the previous year, and (3) the peak in production was earlier in 1959 necessitating the use of more fry tanks throughout the year.

TABLE 2.—*Amount and cost of water used at the Paia hatchery, 1958*

Month	Gallons	Cost [1]	Average cost per month
January–April	[2] 1,792,303	$107.54	$26.88
May	385,752	23.15	23.15
June	634,878	38.09	38.09
July–August	2,239,367	134.36	67.18
September–October	2,540,700	152.44	76.22
November–December	1,692,890	101.57	50.78
Total	9,285,890	557.15	

[1] 6 cents per thousand gallons.
[2] Large volume because of fry-tank leakage.

TABLE 3.—*Amount and cost of water used at the Paia hatchery, 1959*

Month	Gallons	Cost [1]	Average cost per month
February–March	1,214,000	$72.84	$36.42
April–May	2,401,000	144.06	72.03
June–July	3,608,000	216.48	108.24
August–September	2,268,000	136.08	68.04
October–November	2,182,000	130.92	65.46
December	1,427,000	85.62	85.62
Total	13,100,000	786.00	

[1] 6 cents per thousand gallons.

Two air compressors and a system of air lines were installed in March 1959 to aerate the water in the brood tanks and increase its oxygen content during the hours of darkness, when the oxygen content usually reaches a very low level. In April 1959, a 120-foot lead-sheathed, soil-heating cable, rated at 3.65A–220V and capable of producing 800 watts, or 6.7 watts per foot, was installed in each brood tank with the objective of raising water temperatures and inducing early spawning. The amount and cost of electricity used in 1959 for the operation of the filter pump, the air compressors, and the heating cables are given in table 4.

TABLE 4.—*Amount and cost of electricity used at the Paia hatchery, 1959*

Date [1]	Pumps		Heating cables	
	KWH	Cost	KWH	Cost
Mar. 25–Apr. 16	788	$52.64		
Apr. 16–May 18	3,032	165.48		
May 18–June 16	2,158	123.75		
June 16–July 17	832	[2] 25.90	1,794	$32.02
July 17–Sept. 17	116	9.80		[3] 3.11
Sept. 17–Oct. 16	2	1.23		3.11
Total		378.80		38.24

[1] Mar. 27, filter pump placed in use; Apr. 10, heating cable and 1 aerator in use; Apr. 27, second aerator in use; July 1, heating cables turned off; Aug. 10, filter pump turned off.
[2] Heat and power put on separate meters June 13.
[3] Meter service charge.

ENVIRONMENTAL CONDITIONS

Temperature Variations

The monthly averages of maximum and minimum water temperatures in brood-tank A, as measured by a thermograph, are plotted in figures 3 and 4. The daily fluctuation in temperature ranged from 5° to 9° F. In 1958, the highest water temperature was recorded in September and the lowest in December. In 1959, the maximum occurred in July and the minimum in November.

Maximum air temperatures at the Paia station were higher from March through November in 1959 than in 1958 (fig. 5). The minima, on the other hand, were lower in 1959 than in 1958 for the summer months, May through August (fig. 6), but higher for the period February to April. As a result of the generally warmer air conditions during the spring months of 1959, we actually have no way to evaluate the effect of the heating cables on water temperature and spawning.

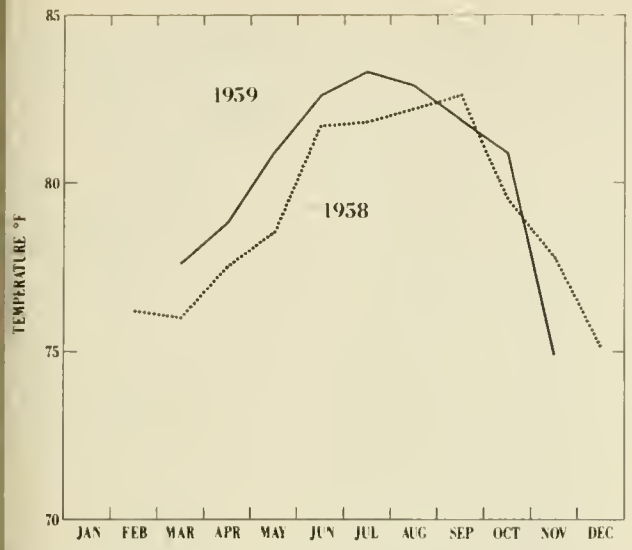

FIGURE 3.—Average monthly maximum water temperatures in brood-tank A in 1958 and 1959.

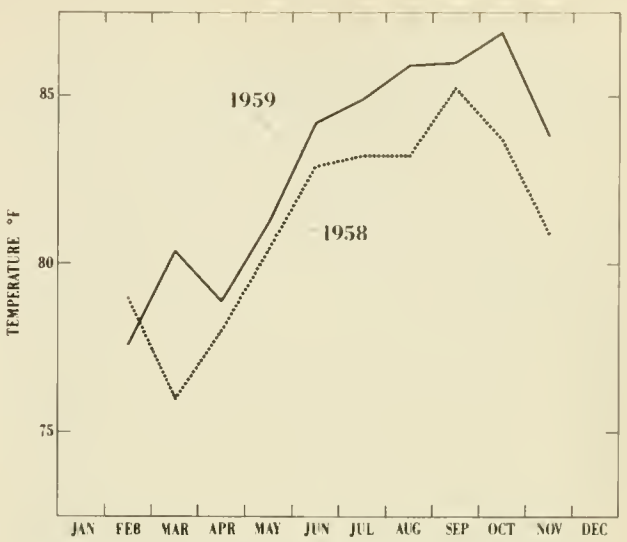

FIGURE 5.—Average monthly maximum air temperatures at Paia, Maui, in 1958 and 1959. (Data courtesy of Hawaiian Sugar Planters Association.)

The two years were generally similar in the amount of sunshine recorded at the Paia station (fig. 7). In the two months March and July, however, there was considerably more sunshine in 1959 than in 1958.

Oxygen Concentrations

1958.—Measurements of the concentration of dissolved oxygen in the brood tanks showed a marked diurnal variation (table 5). Oxygen values at about 8 a.m. were frequently less than 1.0 ml./l., and on a few occasions were less than 0.5 ml./l. These levels are dangerously low and conceivably could have had a detrimental effect on the survival of eggs and young.

On the basis of a 24-hour series of oxygen measurements made in tanks at the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, it would appear that our early morning and afternoon sampling times were close to the hours of minimum and maximum concentrations

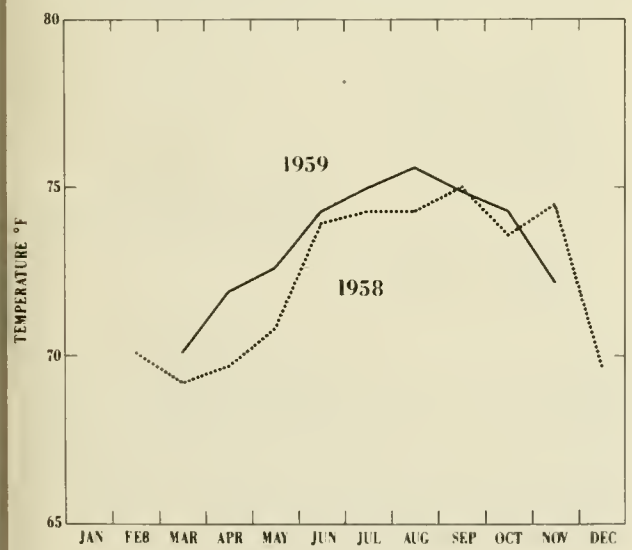

FIGURE 4.—Average monthly minimum water temperatures in brood-tank A in 1958 and 1959.

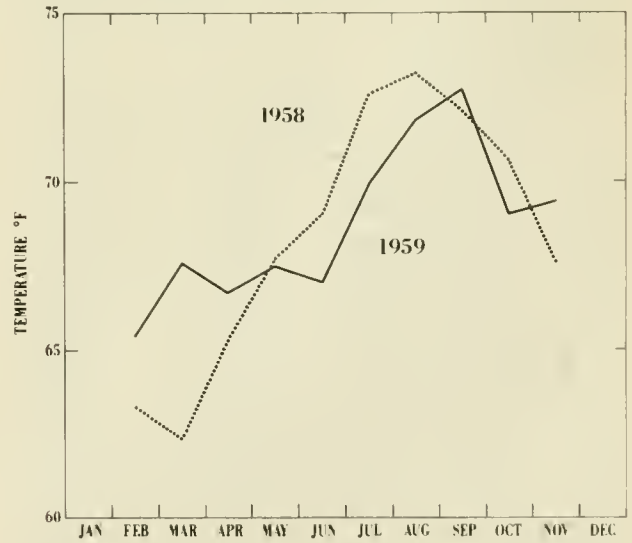

FIGURE 6.—Average monthly minimum air temperatures at Paia, Maui, in 1958 and 1959. (Data courtesy of Hawaiian Sugar Planters Association.)

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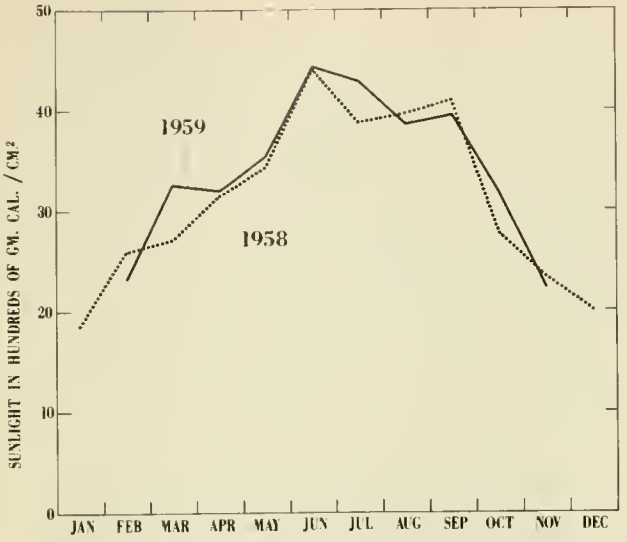

FIGURE 7.—Average monthly sunlight recorded at Paia, Maui, in 1958 and 1959. (Data courtesy of Hawaiian Sugar Planters Association.)

of dissolved oxygen. The low (morning) values averaged 1.11 ml./l. for tank A and 0.99 ml./l. for tank B. The high (afternoon) values averaged 6.62 ml./l. for tank A and 5.12 ml./l. for tank B. This marked diurnal variation resulted, we believe, from oxygen being utilized during the hours of darkness by both algae and fish and being restored during daylight hours by photosynthesis. The difference in tilapia production between the two tanks may possibly have been related to the higher oxygen concentration that prevailed in tank A.

On March 4 and 5, detailed sampling was carried out to determine the differences in oxygen concentration at different positions and at different depths in the brood tanks in relation to inflow and outlet and direction of the prevailing winds. The results are given in table 6. There were no major differences between the two tanks in the afternoon. Early in the morning the oxygen concentrations were slightly less in tank B than in tank A. Concentrations of oxygen were higher at the surface than those midway in the tank, which in turn were usually higher than those near the bottom of the tanks. Concentrations were higher near the inflow end of the tanks than near the outlet, as might be expected.

TABLE 5.—*Concentrations (ml./l.) of dissolved oxygen in selected tanks, measured in morning and afternoon, 1958*

[Samples drawn about 12 in. below surface approximately midway in tank]

Date	Time	Tank A	Tank B	Fry tank No. 90	Remarks
Feb. 12	0830	0.68	0.93	------	
12	1430	6.25	6.98	------	
19	0815	2.68	.39	------	
19	1230	6.36	2.42	------	
26	0830	1.32	1.26	------	
26	1300	5.80	5.49	------	
Mar. 12	0815	.54	.62	4.58	
12	1330	4.49	1.52	4.98	
14	0815	.69	.55	------	Inflow about 4 gal./min.
19	0815	1.44	1.01	4.99	
19	1300	8.49	5.65	6.17	
26	0810	1.30	.65	4.63	
26	1300	8.04	5.05	6.14	
Apr. 2	0815	1.20	.68	4.96	
2	1305	6.77	5.11	6.35	
9	0815	1.26	.82	4.45	
9	1315	7.05	5.55	6.08	
16	0750	1.08	.71	4.20	
16	1300	6.97	5.44	6.71	
23	0750	.86	.60	4.57	
23	1300	5.95	4.78	6.98	
30	0745	.59	.58	3.52	
30	1300	4.62	5.53	6.39	
May 7	0750	.66	.33	3.88	
7	1300	5.64	2.94	6.50	
14	0745	.84	.86	2.68	
14	1300	7.27	6.59	5.61	
21	0745	1.26	1.15	2.55	
21	1320	*9.05	*8.56	5.59	*Water depth 15 in.; sample 3 in. below surface.
28	0630	.40	.49	------	
28	0700	.61	.39	------	
28	0740	.95	1.06	------	
June 5	0620	.35	.50	3.58	Tank A = 2 gal./min. inflow. Tank B = 1 gal./min. inflow.
11	0630	.19	.26	------	
13	0630	.63	.59	------	About 10,000 gal. water passed through each tank overnight.
18	1625	2.64	1.58	------	
25	0630	.52	1.73	------	
July 3	0705	.39	.75	------	
10	0715	1.06	1.08	------	
17	0735	.65	.90	------	
25	0745	.92	.80	------	
Aug. 1	0800	1.24	.78	------	
6	0800	.87	1.05	------	
15	0750	.75	.65	------	
29	0715	.69	1.06	------	
Sept. 4	0750	.89	1.44	------	Inflow of tank B about twice that of A.
12	0725	.66	.76	------	
19	0800	1.36	2.05	------	No water entered brood tanks for past 4 days.
26	0715	.85	1.01	------	
Oct. 3	0800	2.65	1.76	------	
10	0815	4.01	2.01	------	
17	0725	3.96	3.84	------	
24	0735	2.12	1.12	------	
31	0725	2.38	1.63	------	
Nov. 7	0715	.64	.72	------	
14	0725	.64	.52	------	
20	0800	1.29	2.18	------	
26	0805	.83	1.09	------	
Dec. 12	0755	.64	.69	------	Water level lowered in brood tanks; level restored with fresh water Dec. 2–3.
17	0825	.33	.77	------	
26	0745	.49	.52	------	
30	0730	.36	.39	------	

A number of measurements (table 5) taken in one of the fry tanks indicates that oxygen concentrations there were favorable at all times. The high values are related, no doubt, to the shallow depth of the tanks, the high surface area to volume ratio, and the presence of algae.

TABLE 6.—*Concentrations (ml./l.) of dissolved oxygen at different depths and positions in brood tanks, 1958*

Sampling time and depth	Outlet end (NE.)	Middle	Inflow end (SW.)
TANK A [1]			
0815 hours:			
Surface	0.53	0.70	0.76
Midway	.52	.47	.70
Bottom	.42	.40	.66
1330 hours:			
Surface	2.54	3.31	3.46
Midway	2.39	3.29	2.99
Bottom	2.43	3.26	2.97
TANK B [2]			
0830 hours:			
Surface	.73	.51	.34
Midway	.69	.47	.32
Bottom	.67	.48	.18
1315 hours:			
Surface	4.17	3.50	2.99
Midway	3.50	3.42	2.33
Bottom	3.49	3.47	2.18

[1] Sampled March 4.
[2] Sampled March 5.

1959.—In 1959, in contrast with 1958, oxygen concentrations in the brood tanks were usually favorable following installation of the aeration system, with very few readings below 1 milliliter per liter and with the average above 3 ml./l. The very low levels in concentrations of oxygen in some of the fry tanks, however, may have been caused by retention of fish for long periods of time in a single tank with inadequate flushing. The oxygen concentrations in the brood tanks and in selected fry tanks are given in table 7.

TABLE 7.—*Measurements (ml./l.) of dissolved oxygen in selected tanks, taken about midday, 1959*

Sampling date	Brood A	Brood B	Tap	Fry tank No.—						
				76	73	90	86	67	82	66
Mar. 5	4.62	1.29	5.31	-----	-----	-----	-----	-----	-----	-----
13	2.39	1.82	6.26	0.53	-----	-----	-----	-----	-----	-----
17	.83	1.18	4.85	-----	1.18	-----	-----	-----	-----	-----
24	1.50	.95	5.97	.77	.71	-----	-----	-----	-----	-----
31	2.11	2.42	5.21	.45	.60	-----	-----	-----	-----	-----
Apr. 7	3.35	1.77	1.03	.42	1.56	-----	-----	-----	-----	-----
14	2.05	.89	4.99	.16	.58	-----	-----	-----	-----	-----
21	5.36	2.64	5.84	-----	.33	1.72	-----	-----	-----	-----
28	2.04	1.27	4.53	-----	.83	2.44	-----	-----	-----	-----
May 5	3.92	5.18	5.26	-----	1.53	1.78	-----	-----	-----	-----
12	4.01	5.36	5.33	-----	.23	3.41	-----	-----	-----	-----
29	5.89	6.59	5.56	-----	-----	3.65	-----	-----	-----	-----
June 5	5.91	7.17	5.61	-----	-----	-----	-----	6.81	-----	-----
9	5.38	6.18	5.70	-----	-----	-----	-----	3.40	-----	-----
25	5.48	2.80	5.23	-----	-----	-----	5.71	-----	-----	-----
July 7	5.63	5.33	5.25	-----	-----	-----	4.58	-----	-----	-----
14	5.11	4.64	5.76	-----	-----	-----	5.04	-----	-----	-----
22	4.97	3.64	5.46	-----	-----	-----	2.98	-----	-----	-----
28	5.79	4.51	5.40	-----	-----	-----	2.80	-----	-----	-----
Aug. 5	3.47	4.07	3.85	-----	-----	-----	2.75	-----	-----	-----
12	5.66	4.75	5.62	-----	-----	-----	2.92	-----	-----	-----
19	3.56	3.35	4.97	-----	-----	-----	3.78	-----	-----	-----
25	4.27	4.97	5.51	-----	-----	-----	3.54	-----	-----	-----
Sept. 11	5.62	4.03	5.69	-----	-----	-----	-----	3.71	5.80	-----
22	4.39	4.34	4.87	-----	-----	-----	-----	3.19	6.16	-----
29	2.56	2.49	5.08	-----	-----	-----	-----	2.24	2.70	-----
Oct. 8	2.52	2.09	5.08	-----	-----	-----	-----	-----	3.96	4.68
16	1.61	4.90	5.60	-----	-----	-----	-----	-----	3.22	2.38
21	.55	6.18	7.20	-----	-----	-----	-----	-----	5.52	4.56
28	5.08	4.14	5.40	-----	-----	-----	-----	-----	5.08	4.32
Nov. 5	1.89	4.97	5.60	-----	-----	-----	-----	-----	2.24	3.64
13	3.71	1.54	5.81	-----	-----	-----	-----	-----	3.64	2.94
17	2.42	5.69	6.94	-----	-----	-----	-----	-----	5.30	5.54
24	1.92	5.16	5.85	-----	-----	-----	-----	-----	3.41	3.48
Dec. 1	4.39	5.04	5.90	-----	-----	-----	-----	-----	3.38	2.81
Average concentration	3.70	3.81	5.36	.47	.84	2.60	3.79	3.87	4.20	3.82

Other Chemical Determinations

Several chemical determinations were made in 1959 in addition to the oxygen measurements. Data on hydrogen ion concentration (pH), and carbon dioxide (CO_2), bicarbonate (HCO_3^-), and normal carbonate ($CO_3^=$) concentrations are presented in table 8. The slight differences in the pH concentrations in the two brood tanks were judged to be negligible. The CO_2, $CO_3^=$, and HCO_3^- concentrations are approximations, since it was difficult to determine the end points when the water samples were dirty brown to deep green in color, as was frequently the case.

TABLE 8.—*Chemical determinations made on brood tanks, 1959*

Date	Tank A				Tank B			
	pH	CO_2 (p.p.m.)	CO_3 (p.p.m.)	HCO_3 (p.p.m.)	pH	CO_2 (p.p.m.)	CO_3 (p.p.m.)	HCO_3 (p.p.m.)
Mar. 5	8.8	-----	-----	-----	7.9	-----	-----	-----
13	7.6	-----	-----	-----	8.8	-----	-----	-----
17	7.7	-----	-----	-----	7.8	-----	-----	-----
24	8.8	-----	-----	-----	8.8	-----	-----	-----
31	8.8	-----	-----	-----	8.5	-----	-----	-----
Apr. 7	8.3	-----	-----	-----	8.2	-----	-----	-----
14	7.6	-----	-----	-----	7.2	-----	-----	-----
21	7.9	-----	-----	-----	7.4	-----	-----	-----
28	7.9	-----	-----	-----	7.3	-----	-----	-----
May 5	7.6	-----	-----	-----	8.0	-----	-----	-----
12	8.2	4.26	22	142	8.6	2.18	5	35
29	8.6	-----	-----	-----	8.2	-----	-----	-----
June 5	7.8	-----	-----	-----	8.1	-----	-----	-----
9	7.8	4.0	0	102	7.8	1.7	0	97
25	7.9	10.5	0	14.5	8.6	8.0	0	17.5
July 7	7.9	9.0	0	130	8.4	4.0	0	63
14	7.9	13.0	0	111	8.8	0	15	65
22	7.8	4.5	0	88.5	8.4	4.0	0	42.5
30	8.2	4.0	0	105	8.0	5.0	0	65
Aug. 5	7.6	10.5	0	94	7.6	12.5	0	90
12	8.2	5.6	0	94	8.8	4.0	0	77
19	7.8	12.0	-----	135	7.8	9.5	0	88
25	9.0	2.5	0	110	8.8	7.0	0	90
Sept. 11	7.6	10.0	0	83	7.4	9.0	0	69
22	7.6	12.5	0	91	7.4	9.5	0	100
29	7.3	15.2	0	81	7.2	15.1	0	71
Oct. 8	7.6	11.5	0	84	7.3	11.0	0	73
16	7.5	12.0	0	86	7.4	6.0	0	52
21	7.2	10.0	0	99	7.4	7.0	0	66
28	7.4	7.5	0	70	7.2	9.5	0	81
Nov. 5	7.2	10.0	0	86	7.4	15.0	0	55
13	7.2	7.0	0	54	7.2	10.0	0	68
17	7.2	6.5	0	72	7.2	4.0	0	39
24	7.2	8.0	0	74	7.5	4.5	0	38
Dec. 1	7.2	11.0	0	70	7.4	8.0	0	60
Maximum	9.0	15.2	-----	142	8.8	15.1	-----	100
Minimum	7.2	2.5	-----	14.5	7.2	0	-----	17.5

OPERATION OF THE HATCHERY

STOCKING THE BROOD TANKS

The brood stock for stocking the tanks was supplied by Hawaiian Tuna Packers, Ltd. The crew of the sampan *Amberjack* seined the fish on January 10, 1958, from reservoir No. 6, at Ewa, Oahu. The fish were acclimatized to sea water in the bait wells of the sampan and transported to Maui on January 11–12. Some mortalities occurred during the acclimatization and as a result of handling, but about 5,000 fish weighing 1,200 pounds survived. A total of 2,000 adults (500 males and 1,500 females), weighing 625 pounds, were stocked in the two brood tanks, each tank receiving 250 males (0.34 lb. average weight) and 750 females (0.30 lb. average weight). The remainder of the fish were retained to replace stock that died.

In the days that followed, dead fish were removed from the tanks and replaced with a like number of the appropriate sex. Deaths were numerous during the first week after stocking, but were practically zero by the end of the second week. The total mortality from January 13 to 31 was 705 fish (549 females and 156 males). The mortality rate was about the same for the sexes.

The adult fish were stocked in 1958 at a concentration of 1 male per 3.37 square feet of bottom area. Uchida and King (1962) had found that production was favorable in tanks where the area allotted per male was about 3 square feet. Although in their initial experiments Uchida and King used a 2 ♀ : 1 ♂ sex ratio with successful results, it was anticipated that better production might be obtained by increasing the ratio to 3 ♀ : 1 ♂, so we used this latter ratio.

Although the area was fenced and posted, vandals entered the hatchery on September 25 and 27, 1958, removing an unknown number of adult fish. As we did not wish to disturb the fish further, we postponed taking a census until December 2–3, 1958, when production had declined. A census on these dates showed that brood-tank A contained 689 females and 216 males, a loss of 61 females and 34 males since stocking. Brood-tank B contained 736 females and 251 males, a loss of 14 females and a gain of 1 male (this apparent gain may have been due to miscount or to recruitment of a juvenile that escaped capture and grew to adulthood).

In later experiments in 1958, Uchida and King found that the best production of fry was observed in tanks with a 3 ♀ : 1 ♂ ratio and with about 4 square feet of bottom area per male. Therefore, in 1959 we stocked each brood tank with 600 females and 200 males, with each male being allotted 4.21 square feet of bottom area. A census taken on December 7–8, 1959, showed that tank A contained 604 females and 228 males, a gain of 4 females and 28 males. Brood-tank B contained 668 females and 252 males, an increase of 68 females and 62 males. These increases were due, we believe, to recruitment of juveniles that had escaped capture early in the year and had grown to maturity. The males averaged 30.5 centimeters (12 in.) in length and 1.0 pound in weight, while the females averaged 22.9 cm. (9 in.) in length and 0.5 pound in weight when the brood stock was counted in December 1959.

FEEDING SCHEDULES

Adults

In 1958, the brood stock was usually fed twice daily except on Sundays. The fish were fed once every Sunday until June and were not fed on Sundays thereafter. The daily ration for the total brood stock ranged from 5 to 12 pounds, depending on how readily the fish were feeding. An average daily ration of 4 pounds of Purina trout chow (developer) per 1,000 adults seemed to satisfy the needs of the fish during their most productive period. The kinds of feed used in 1958, with the price per pound, are shown in table 9. In January to March, 1958, the adults were fed a millrun-fish meal mixture (4:1 ratio). In April, the feed in one brood tank (B) was changed to rabbit ration (pelletized), a better quality feed. The change in feed did not result in an increase in fry production. The rabbit ration was supplemented in July with Purina trout chow and in August through December 1958 the fish in both brood tanks were given Purina feed.

In 1959, the brood stock was fed twice daily, except on Sundays, from February through October, and once daily from November through December. They were fed once on Sundays until May and were not fed thereafter on Sunday. Their daily ration was 3 to 6 pounds of Purina developer or large fingerling feed. The kinds, costs, and amounts of feed used in 1959 are shown in table 10.

TABLE 9.—*Amount (in pounds) and cost of feeds supplied tilapia brood stocks, 1958*

Month	Fish-meal	Millrun	Clark's crumbles	Mid-dlings	Fresh liver	Rabbit ration	Purina trout chow	Purina small finger-ling	Total amount	Total cost
January	17.5	71.3	19.5	76.7					185.0	$12.64
February	26.5	106.0	32.5						165.0	14.08
March	40.6	162.4							203.0	8.12
April	26.8	111.2			1.8	67.0			206.8	10.58
May	27.2	108.8				148.0			284.0	14.32
June	21.0	84.0				105.0			210.0	10.50
July	20.4	81.6				57.0	45.0		204.0	13.35
August	3.0	12.0					165.0		180.0	22.05
September							153.0		153.0	19.89
October							161.0		161.0	20.93
November							120.0	52.0	172.0	22.36
December								178.0	178.0	23.14
Total amount (lb.)	183.0	737.3	52.0	76.7	1.8	377.0	644.0	230.0	2,301.8	
Average cost per pound	$0.08	$0.03	$0.27	$0.05	$0.60	$0.06	$0.13	$0.13		
Total cost	14.64	22.12	14.04	3.84	1.08	22.62	83.72	29.80		191.96

TABLE 10.—*Amount (in pounds) and cost of feeds supplied tilapia brood stocks, 1959*

Month	Purina developer	Purina large fingerling	Total amount	Total cost
March	168.10		168.10	$21.85
April	100.00	34.50	134.50	17.48
May	29.25	88.75	118.00	15.34
June		117.00	117.00	15.21
July		142.50	142.50	18.53
August		163.75	163.75	21.29
September		132.00	132.00	17.16
October		132.00	132.00	17.16
November		96.00	96.00	12.48
December		16.00	16.00	2.08
Total amount (lb.)	297.35	922.50	1,219.85	
Average cost per pound	$0.13	$0.13		
Total cost	38.66	119.92		158.58

The adults generally fed avidly when production of young was low but not when production was high.

Young

The young fish were usually fed three times daily in 1958, except on Sundays, with the amounts varying with the number and age of the young. Our intention was to give the fry all the feed they could consume in order to obtain maximum growth. Toward the end of summer, with about 500,000 young in the tanks, 45 pounds of feed were supplied daily.

Until they were 2–3 weeks of age, the very young fish paid little attention to the feed offered them, feeding principally on green algae obtained from the walls of the tanks. The kinds, amounts, and costs of feed supplied the young fish in 1958 are listed in table 11. Until July, the young fish were fed primarily on Clark's trout feed and a wheat middlings-fish meal mixture (4:1 ratio). Starting in July this was supplemented with Purina trout feed. The use of Clark's feed was discontinued in September.

The young fish were usually fed twice daily in 1959 with rations similar to those in 1958. The very young to 3-week-old fish were fed on either Purina starter or a middlings–fish-meal mixture (4:1 ratio). The 3- to 10-week-old fish were fed on Purina fry feed. The 10-week-old and older fish were fed a mixture of millrun-fish meal (4:1 ratio). The kinds, amount, and cost of various feeds given the young in 1959 are listed in table 12.

We did not attempt to record the amount of feed supplied to the fish in each fry tank because the tanks were too numerous and the fish varied among tanks from newly hatched fry to bait-size fish. At each feeding the fish were given the maximum amount that they would consume, based on past observations. The total weight of feed given the young at each feeding was recorded. With experience gained during the 2 years of operation, we were able to set up a feeding schedule that appeared adequate for favorable growth. The schedule outlined here is suitable for a tank 6.5 × 11 feet containing approximately 6,500 young. The amounts specified should be given 2 or 3 times daily as follows:

First and second weeks, 0.3 ounces per feeding; third week, 0.8 oz.; fourth and fifth weeks, 1.3 oz.; sixth and seventh weeks, 2.5 oz.; eighth week and older, 5.9 oz. per feeding. With three feedings a day, 6 days a week for 12 weeks, 43.3 pounds of feed were required to produce about 18 pounds of bait-size fish, or 2.4 pounds of feed per pound

TABLE 11.—*Amount (in pounds) and cost of feeds supplied tilapia fry, 1958*

Month	Clark's crumbles	Fish-meal	Mid-dlings	Rabbit ration	Beef liver	Fresh skipjack	Purina fry feed	Purina small finger-ling	Purina trout chow	Total amount	Cost
March	0.1	0.3	1.2							1.6	$0.11
April	3.0	.7	3.2	0.3	0.1					7.3	1.10
May	7.6	1.6	6.3	4.3						19.8	2.75
June	33.3	8.3	33.2	3.0						77.8	11.50
July	60.3	38.1	156.2	.3		14.0	68.5			337.4	36.06
August	26.0	109.0	436.0				33.0	156.5		760.5	62.18
September	23.0	181.5	726.0						22.0	952.5	59.89
October		130.8	523.2				61.0	74.0		789.0	54.17
November		82.0	328.0				190.0	76.0		676.0	57.54
December		55.0	230.0				392.0	181.0		858.0	90.39
Total amount (lb.)	153.3	607.3	2,443.3	7.9	0.1	14.0	744.5	487.5	22.0	4,479.9	
Average cost per pound	$0.27	$0.08	$0.05	$0.06	$0.60	Free	$0.13	$0.13	$0.13		
Total cost	41.39	8.58	122.16	.47	.06		96.79	63.38	2.86		375.69

TABLE 12.—*Amount (in pounds) and cost of feeds supplied tilapia fry, 1959*

Month	Mill-run	Wheat mid-dlings	Purina starter	Purina fry	Fish meal	Total amount	Total cost
March	25.65	[1] 225.72				251.37	$12.06
April	147.80	30.69	12.63	71.15		262.27	16.86
May	59.18	48.90	48.90	177.68		334.66	33.68
June		46.20	9.40	560.00		615.60	76.33
July		258.50	75.00	268.00	51.00	652.50	61.59
August		352.00	8.00	280.00	103.00	743.00	63.28
September			9.00	398.00		407.00	52.91
October			7.25	420.00		427.25	55.54
November			5.75	474.00		479.75	62.37
December			1.00	88.00		89.00	11.57
Total weight	232.63	962.01	176.93	2,736.83	154.00	4,262.40	
Average cost per pound	$0.03	$0.05	$0.13	$0.13	$0.08		
Total cost	6.98	48.10	23.00	355.79	12.32		446.19

[1] High quantities fed bait-size fish carried over from 1958.

of bait-size fish. These amounts do not include natural foods occurring in the ponds, such as green algae and mosquito and midge larvae, which were consumed in some quantity by the young fish.

COLLECTING THE FRY

Once production had started, a diligent effort was made each day to remove all the young that could be captured by dipnetting. A sorting device consisting of a large net mounted behind a frame with grating of aluminum tubing, which was to be pulled through the brood tanks, was tried but did not prove feasible. The device was effective in catching young fish but was judged impractical because of the problem of removing the young from the net and from the detritus that was also collected. Since the young schooled near the surface of the water, dipnetting with a square-framed, 20 × 20-inch net "walked" along the walls of the brood tanks was a simple and satisfactory method of collection (fig. 8). The young were transferred from the dipnet to a bucket and then counted and released into the fry tanks. Each fry tank was stocked with about 6,500 young, or 91 young per square foot of surface area. Some effort was made to put fry of the same size into each tank to reduce cannibalism. The few young that escaped the daily dipnetting were removed at intervals of 3 to 4 months when we seined the ends of the brood tanks where the juveniles tended to congregate.

FIGURE 8.—Dipnetting tilapia fry.

TABLE 13.—*Monthly production of young tilapia in brood-tanks A and B, 1958*

Month	Number of young			Number of young per female			Young produced per square foot of area		
	Tank A	Tank B	Total	Tank A [1]	Tank B [2]	Average	Tank A	Tank B	Average
January									
February	698	240	938	0.9	0.3	0.6	0.8	0.3	0.6
March	8,640	11,550	20,190	11.5	15.4	13.4	10.3	13.7	12.0
April	15,626	5,003	20,629	20.8	6.7	13.8	18.6	5.9	12.2
May	21,006	10,162	31,168	28.0	13.5	20.8	24.9	12.1	18.5
June	122,427	40,444	162,871	163.2	53.9	108.6	145.4	48.0	96.7
July	151,570	108,227	259,797	202.1	144.3	173.2	180.0	128.5	154.2
August	119,296	80,453	199,749	159.1	107.3	133.2	141.7	95.5	118.6
September	128,999	39,113	168,112	172.0	52.2	112.1	153.2	46.5	99.8
October	97,053	35,055	132,108	140.9	47.6	94.2	115.3	41.6	78.4
November	23,682	33,657	57,339	34.4	45.7	40.0	28.1	40.0	34.0
December	15,072	6,103	21,175	21.9	8.3	15.1	17.9	7.2	12.6
Total	704,069	370,007	1,074,076	954.8	495.2	725.0	836.2	439.3	637.6

[1] Tank A contained 750 females during the January–September period and 689 females during October–December.
[2] Tank B contained 750 females during January–September period and 736 females during October–December.

PRODUCTION OF YOUNG

The monthly fry production is given in table 13 for 1958 and in table 14 for 1959. These data are based on gross production and do not indicate losses from disease, cannibalism, or other factors. There was marked seasonal variation with the peak production in 1958 occurring in July and in 1959 in May.

There was an important difference in the production of the two brood tanks in 1958 that may have been related to the position of the inlets and drains, the direction of the prevailing winds, and the resultant circulation of the water within the tanks. Tank A, with the drain on the upwind side, was generally cleaner and more productive than tank B, which had the drain on the downwind side. In 1959 a drain was installed on the upwind end of tank B and the water was somewhat cleaner than in the previous year.

Production was higher in 1959 than in 1958 and there was little difference between the two tanks. Factors operating in 1959 which may have contributed to the higher production that year were—

1. Improved drainage in brood-tank B.
2. Larger bottom area (4.21 sq. ft. versus 3.37 in 1958) allotted to each male.
3. Aeration of the brood tanks.
4. Water filtered and recirculated in brood-tank A.
5. Slightly higher water temperatures. Since both brood tanks were heated slightly and there were no control tanks, it is difficult to evaluate the results. We can state, however, that water temperatures rose following installation of the heating cables (figs. 4 and 5) and that production increased over that of the previous year.
6. Increased oxygen content in brood tanks.
7. Higher grade of feed fed adults.

TABLE 14.—*Monthly production of young tilapia in brood-tanks A and B, 1959*

Month	Number of young			Number of young per female [1]			Young produced per square foot of area		
	Tank A	Tank B	Total	Tank A	Tank B	Average	Tank A	Tank B	Average
January									
February	1,706	0	1,706	2.8	0	1.4	2.0	0	1.0
March	7,396	20,280	27,676	12.3	33.8	23.0	8.8	24.1	16.4
April	112,167	138,215	250,382	186.9	230.4	208.6	133.2	164.1	148.7
May	164,671	129,179	293,850	274.5	215.3	244.9	195.6	153.4	174.5
June	96,135	55,851	151,986	160.2	93.1	126.6	114.2	66.3	90.2
July	59,331	64,151	123,482	98.9	106.9	102.9	70.5	76.2	73.4
August	71,929	53,241	125,170	119.9	88.7	104.3	85.4	63.2	74.3
September	116,781	91,493	208,274	194.6	152.5	173.6	138.7	108.7	123.7
October	52,259	11,908	64,167	87.1	19.8	53.4	62.1	14.1	38.1
November	38,471	5,745	44,216	64.1	9.6	36.8	45.7	6.8	26.2
December	2,477	348	2,825	4.1	0.6	2.4	2.9	0.4	1.6
Total	723,323	570,411	1,293,734	1,205.4	950.7	1,077.9	859.1	677.3	768.1

[1] Based on 600 females in each brood tank throughout the year.

8. Better physical condition of brood stock than in 1958, when they were captured and transported from Oahu to Maui.

9. Larger size of brood fish, which may have been responsible for the larger number of young produced per female (Chen, 1953; Vaas and Hofstede, 1952).

In 1958, newly released fry were observed in February, 1 month after the initial stocking of the adults. Production remained at a low level, however, from February to May. Heavy production started in June and continued through October. In 1958, the highest number of young collected in any one day was 29,800 fry on July 8th. The average production per female for the year was 725 fry.

In 1959, production was at a low level in February and March, but remained high from April through September. The largest day's collection of fry in 1959 was 40,877 fry on May 19th. The average production per female for the year was 1,078 fry.

MORTALITY OF YOUNG

Many factors contributed to the loss of young fish. Some of the observed mortalities were due to handling, disease, and to structural failures such as tank leaks. Many sources of attrition such as predation by black-crowned night herons, dragonfly nymphs, and adult tilapia, and cannibalism among the fry themselves, were known to exist but difficult to estimate. Table 15 provides monthly figures for the dead fish that were collected and counted. In 1958, such losses totaled 48,806, or 4.5 percent of the gross production. The unobserved mortalities for 1958 amounted to 82,400,[1] or 7.7 percent of the gross production. The estimated total mortality was 131,200 or 12.2 percent. Losses in 1959 totaled 99,209, or 7.7 percent of the gross production. The unobserved mortalities for 1959 amounted to 71,800, or 5.6 percent, for a total mortality of 171,000, or 13.2 percent.

As far as we could determine, the brood tanks remained disease free in 1958. In 1959, a minor outbreak of the protozoan *Trichodina* caused some loss of very young fry before the infected individuals were removed. In the young fish, the major disease problems resulted from infections of *Trichodina*, which were controlled by treatment with 0.5 p.p.m. copper sulphate or 3 p.p.m. potassium permanganate. A condition diagnosed as acute catarrhal enteritis, as described by Davis (1956), was the cause of high mortality rates in a few of the tanks. Losses from disease were minimized by the fact that each of the 90 fry tanks had an independent water supply and did not drain into any of the other tanks. Except in brood-tank A, none of the water used was recirculated in 1959. This may not have been the most economical use of water, but it did prevent infections from spreading from one tank to another.

On the few occasions in 1958 when the water supply was interrupted by breaks in the line, there were particularly serious outbreaks of disease. Such water shortages did not occur in 1959. Chemical treatment followed by a thorough flushing with fresh water usually brought an end to the losses in 2 or 3 days. Highest mortality rates occurred when the fish were 1 to 3 weeks old. Once past their 4th week, tilapia seemed to be immune to the usual disorders.

Early detection and treatment of disease were necessary to keep losses at a low level. Treatment with 3 p.p.m. potassium permanganate was effective for fish 0–2 weeks old infected with *Trichodina*, and 0.5 p.p.m. copper sulphate was effective for fish 3 weeks old and older. Treatment was applied usually between the hours of 9 a.m. to 3 p.m., when the oxygen content of the water in the fry tanks was highest, so that the young would have an adequate oxygen supply during treatment.

TABLE 15.—*Observed mortalities of young tilapia, by months, 1958 and 1959*

Month	1958		1959	
	Brood tanks	Fry tanks	Brood tanks	Fry tanks
January				
February	221	9		
March	271	4,006	148	[1] 391
April	8	2,317	974	[2] 53,586
May	48	3,004	423	20,186
June	95	323	227	4,577
July	105	6,872	86	471
August	33	4,412	130	2,269
September	124	[3] 15,119	170	2,300
October	26	[4] 8,521	0	6,996
November	26	1,464	422	5,853
December	0	1,802		
Total	957	47,849	2,580	96,629

[1] 233 lost from fry-tank leakage.
[2] 4,170 lost from fry-tank leakage; 35,373 died after treatment with pyridylmercuric acetate.
[3] 6,555 were lost when a hole opened in the bottom of a fry tank, draining the tank.
[4] 5,967 were lost in the same manner as in footnote 3.

[1] Method of calculating this figure explained in section dealing with the production of bait-size fish.

Fish afflicted with the condition diagnosed as acute catarrhal enteritis were supplied with an increased flow of fresh water, since there is no known treatment.

In 1959, each newly filled tank was given a prophylactic treatment of 3 p.p.m. potassium permanganate or 0.5 p.p.m. copper sulphate before the fry were added. This procedure seemed to be effective in checking *Trichodina* outbreaks. Although we have no measure of the effect of wind-blown dust and debris on the disease problem, we believe that the causative organisms of some of the infections could have been introduced through the excessive amounts of road dust that occasionally contaminated the tanks. Early detection of disease was often difficult because of rain or strong winds that prevented our observing the condition of the fish.

DUTIES OF THE HATCHERY OPERATOR

When operated on an experimental basis, the Paia plant required one person full time; on a commercial basis we estimate that the work load would not have been too great for one man half time.

The daily tasks and time required to perform them were as follows:

1. Dipnetting the young—½ hour to 2 hours.
2. Counting the young—½ hour to 3 hours.
3. Feeding adult fish twice a day—¼ hour.
4. Feeding young three times a day—¼ to ½ hour.
5. Removing the dead fish—10 minutes to 3 hours.
6. Checking inflow and drain pipes—¼ to ½ hour.

Some irregularly occurring tasks were as follows:

1. Treating sick fish: weighing chemicals, applying treatment, checking results, flushing out tanks with fresh water—½ hour to 4 hours.
2. Transferring young from fry tanks to holding tanks—2 men ½ day a week during productive season.
3. Cleaning fry tanks—½ day a week.
4. Constructing equipment, mending nets, et cetera—2 hours a week.
5. Measuring oxygen concentrations—1 hour if done once a week.
6. Caring for grounds—1 day every 4 weeks with power mower.
7. Trucking bait-size fish to docksite—truck driver and helper, 1 day a week during productive season.
8. Acclimatizing bait fish—Old method: 1 day a week during productive season. New method: 4 hours a week during productive season.

PRODUCTION OF BAIT-SIZE TILAPIA

1958 PRODUCTION

By the end of December 1958, an estimated 412,530 bait-size (1.5 to 2.5 in.) tilapia, weighing 1,429 pounds (204 buckets[2]), had been removed from the hatchery. Of this amount, 189,237 fish weighing 630 pounds (90 buckets) were delivered to Maui Fisheries and Marine Products, Ltd.: the rest were used in experimental fishing from the Bureau of Commercial Fisheries research vessels *Hugh M. Smith* and *Charles H. Gilbert*. On January 8, 1959, an estimated 146,346 fish weighing 531 pounds (76 buckets) were received aboard the *Smith* and the *Gilbert*. The average individual weight of fish in each of the delivered lots, estimated by subsampling, ranged from 1.17 grams (39 mm. or 1.5 in. length) to 2.18 g. (49 mm. or 1.9 in. length). The overall average weight was 1.59 g. (44 mm. or 1.7 in. length).

If we subtract from the estimated total production (1,074,076) the number of fish delivered (558,876) up to January 8, 1959, and the observed mortality (48,806), we obtain a remainder of 466,394 fish, the theoretical balance on hand. Following the January 8th delivery to the *Smith* and *Gilbert*, 64 fry tanks each containing an estimated 6,000 young fish approaching bait size remained at the Paia plant. This stock of 384,000 fish, barring accident, should equal 190 buckets of bait by the end of February. The difference between 466,394 and 384,000 equals 82,394 or the unobserved losses resulting from cannibalism, predation by night herons and dragonfly nymphs, and from other causes. In terms of buckets, the total production, therefore, amounted to 470 buckets. In terms of production per unit area, the 1958 production was equal to 9,200 pounds (4.6 tons) of fish per acre per year, based on the 280 buckets actually used, or 15,400 pounds (7.7 tons) per acre per year, based on the estimated total production.

[2] One bucket equals 7 pounds of fish.

1959 PRODUCTION

By the end of December 1959, an estimated 767,071 bait-size (1.5 to 2.1 in.) tilapia weighing 2,489 pounds (356 buckets) had been removed from the hatchery. Of this amount 508,364 fish weighing 1,415 pounds (202 buckets) were delivered to Maui Fisheries and Marine Products, Ltd. A few buckets of fish were supplied to the Hawaii Division of Fish and Game for experimental purposes. The rest were used from the *Smith* and *Gilbert*. The average individual weight of fish in each of the delivered lots, estimated by subsampling, ranged from 0.92 g. (37 mm. or 1.5 in. length) to 2.67 g. (52 mm. or 2.1 in. length). The average of all lots was 1.49 g. (43 mm. or 1.7 in. length). Of the total bait delivered, 159,504 fish or 971 pounds were carried over from the 1958 production.

The total production for 1959 was 1,293,734 fry. If we subtract the observed mortalities (99,209) and fish delivered (607,567) from the total production, we have a remainder of 586,958 fish. An estimated 514,900 fry remained in the hatchery as of December 8, 1959. The difference between 586,958 and 514,900 is 72,058 fish, representing the unobserved losses from cannibalism, predation by night herons and dragonfly nymphs, and other causes. In February 1960, 257 buckets of bait should have been available at the hatchery. The total bait delivered during 1959 was 1,517.9 pounds (216.8 buckets), and the production was equal to 7,110 pounds (3.6 tons) per acre per year on an area basis, or 15,600 pounds (7.8 tons) per acre per year based on the total estimated production. Production in numbers of young was higher in 1959 than in 1958, but production in buckets of bait was about the same in the two years, since the average size of the fish was smaller in 1959. The smaller average size in 1959 may have resulted from the less-frequent feeding and greater stocking densities.

There are numerous reports dealing with the pond culture of tilapia. Chen (1953) reported an annual production of 270 pounds per acre in the rice paddies of Taiwan, and Pongsuwana (1956) reported annual productions in excess of 5 tons per acre in Thailand. Swingle (1960) reported annual productions of 2,291 and 9,685 pounds per acre in Alabama from stocking rates of 4,000 and 20,000 fingerlings per acre, respectively, basing the production on 365 growing days a year.

ACCLIMATIZATION TO SEA WATER

The bait-size tilapia were hauled by truck from the Paia hatchery to a docksite area, either to Maalaea Harbor or to Kahului Harbor. Two means were used to transport the fish: (1) 50-gallon drums, each with a carrying capacity of 1 to 1.5 buckets of fish, and (2) a special truck bearing a 500-gallon steel tank having a carrying capacity of about 10 buckets of bait.

The acclimatization to sea water was carried out either in large wooden tanks equipped with running fresh and salt water, located at Maalaea Harbor (fig. 9), or in the bait wells of the sampans and the Bureau of Commercial Fisheries vessels. In each instance, the acclimatization was accomplished in 8 to 12 hours and with little loss of fish, except for one unfortunate experience when an entire lot of 129 pounds (27,000 fish) died. Mortality in this case was probably the result of a combination of factors: the rate of change from fresh water to sea water was too rapid; there was insufficient fresh water available to permit proper acclimatization and the maintenance of suitable oxygen concentrations; the vessel, lying at the dock in Maalaea Harbor and, being held against the dock by the wind, was generally motionless, so there was little circulation of water through holes in the bottom of the bait wells. The loss was regrettable but taught us several things about the requirements and limitations of the fish that must be considered during the acclimatization process.

FIGURE 9.—Tilapia acclimatization tanks at Maalaea Harbor, Maui.

In 1959, Maui Fisheries and Marine Products, Ltd., built a concrete and hollow-tile tank, 10 feet × 30 feet × 3 feet deep, at Maalaea Harbor, which was capable of holding about 30 buckets of fish. The fish were acclimatized in this tank by introducing them directly into water with a salinity of approximately 17 °/₀₀ and leaving them at this salinity for at least 12 hours before introducing them into sea water (35 °/₀₀) in the bait wells of the sampans. This method, developed by the Hawaii Division of Fish and Game in 1959 (unpublished data), was easy to follow and usually resulted in few losses. One great advantage was that no one needed to monitor the salinity and regulate continually the flow of salt and fresh water, as was required for the method employed in 1958. The water in the acclimatization tank was aerated by a small compressor, with a few airstones distributed over the bottom of the tank.

UTILIZATION OF BAIT

The results of fishing operations utilizing tilapia produced at the Paia hatchery along with the naturally occurring bait fishes, nehu and iao, are presented in table 16. The amount of bait used was estimated by the fishermen. An observer accompanied the vessels on most of the trips and recorded the catch rates with the different types of baits used.

We calculated an average catch of 49 pounds of skipjack per pound of tilapia used in 1958, as compared with 48 pounds of skipjack per pound of nehu and 68 pounds of skipjack per pound of iao. In 1959, the average catch amounted to 53 pounds of skipjack per pound of tilapia, and 64 pounds of skipjack per pound of nehu. Iao was used on one trip with a catch of 49 pounds of skipjack per pound of iao. Although most of the catches were made using nehu and tilapia alternately, some schools were fished entirely with tilapia with fairly good results. On September 5, 1959, the *Sailfish* caught 5,600 pounds of 20-pound skipjack using 90 pounds of tilapia, or 62.2 pounds of skipjack per pound of tilapia.

These results indicated that tilapia could be used to advantage to supplement the supplies of nehu. The fishermen commented on the fact that tilapia were slow swimmers, and necessitated reducing the speed of the sampans during the chumming and fishing operations. Also, they noted that the tilapia were very hardy and performed well when large wild schools of skipjack were encountered, and that they were particularly good bait for large skipjack of 18 to 25 pounds.

TABLE 16.—*Tilapia as skipjack bait compared with nehu and iao, 1958 and 1959*

Vessel and date	Bait taken aboard (lb.)			Bait used (lb.)			Skipjack catch (lb.)		Catch rate					
									Number of skipjack per pound of bait used			Pounds of skipjack per pound of bait used		
	Nehu	Tilapia	Iao	Nehu	Tilapia	Iao	Total weight	Average weight of fish	Nehu	Tilapia	Iao	Nehu	Tilapia	Iao
1958:														
Amberjack: July 22	117	54		117	32		4,110	8.1	3.8	2.0		30.7	16.2	
Olympic:														
Aug. 25	99	54		99	45		9,000	22.1	3.1	2.2		68.8	48.6	
Aug. 30		72	50		40	45	4,500	17.6		3.0	3.0		53	52
Sept. 4	45	32	72	45	32	54	9,000	14.0	3.2	5.7	6.0	44.4	79.2	83.3
Average									3.4	3.2	4.5	48.0	49.2	67.6
1959:														
Tradewind:														
July 8	36	18		34	2		6,708	12.0	16.5	0.4		198.0	4.8	
July 10	270	27		180	18		9,100	16.0	3.1	0.3		50.0	5.0	
Sooty Tern: July 10	300	60		276	12		18,030	15.0	4.3	0.2		65.0	2.5	
Sailfish:														
July 30	234	108		90	18		5,600	18.3	3.1	1.5		56.7	27.5	
July 31	144	90		144	81		6,943	13.3	3.1	1.0		40.9	13.0	
Buccaneer:														
Aug. 10	324	117		63	14		4,429	25.6	1.4	6.1		37.0	156.2	
Aug. 11	261	104		238	22		10,114	16.8	1.9	6.3		32.5	105.3	
Aug. 12	22	81		22	63		5,120	16.0	2.5	4.2		39.8	67.0	
Sailfish:														
Aug. 27	90	108		90	108		15,000	(1)	(1)	(1)		55.5	92.5	
Sept. 5		90			90		5,600	20.0		3.1			62.2	
Olympic: Sept. 7		90	81		90	81	9,500	22.0		2.3	2.2		50.0	49.4
Average									4.5	2.5	2.2	63.9	53.3	49.4

[1] No records.

SUMMARY OF PRODUCTION COSTS

The major elements in the cost of producing a pound or a bucket of bait-size tilapia in each of the two years of the operation are described in the sections that follow and are summarized in table 17.

TABLE 17.—*Summary of production costs, 1958 and 1959*

Item	1958	1959
Capital improvements	$4,353.24	$900.00
Annual cost, amortized on a 10-year basis	435.32	525.32
Interest on capital investments	261.19	315.19
Operating expenses	1,814.82	2,507.79
Total cost	2,511.33	3,348.30
Number of fry produced	1,074,076	1,293,734
Production of bait-size fish:		
Number of buckets	470	474
Number of pounds	3,290	3,318
Cost per pound	$0.76	$1.01
Cost per 7-pound bucket	$5.34	$7.06

1958 OPERATIONS

An accounting of the major expenses incurred in setting up and operating the plant at Paia during the first year, not including the salary of a biologist, follows.

In addition to the operating expenses incurred in 1958, it was necessary to supply feed and water for approximately 2 months in 1959 to the young fish that were held over from 1958.

Capital improvements:[1]	
Initial renovation of the plant	$2,233.24
Other construction and improvements	1,500.00
Barbed-wire fencing	90.00
Bait-hauling tank	100.00
Bait acclimatization facilities	380.00
Bait-barge acquisition and repair	50.00
Total	4,353.24
Operating expenses:	
1958:	
Feed—for adult fish	$191.96
Feed—for young fish	375.69
Water	557.17
Hauling bait fish to docksite	90.00
Maintenance and care of grounds	150.00
Annual lease on plant area	240.00
Subtotal	1,604.82
1959:	
Feed—for young fish	$60.00
Water—for fry tanks	50.00
Hauling bait fish to docksite	100.00
Subtotal	210.00
Total	1,814.82

[1] Borne by Maui Fisheries and Marine Products, Ltd.

It is customary to amortize the cost of capital improvements over a reasonable period of time. We suggest amortizing the costs over a 10-year period in this instance, rather than charging the full amount against the quantity of bait produced the first year. Also, it is usual business procedure to include in the cost analysis a figure representing income that might be derived from a reasonable interest rate on the capital cost of the original construction; i.e., income which might have been realized had the money been invested. A 6-percent return on the amount of the capital improvements ($4,353.26) would equal $261.19.

Total costs:	
Capital improvements	$435.32
Interest	261.19
Operating expenses:	
Jan.–Dec., 1958	1,604.82
Jan.–Feb., 1959	210.00
Total	2,511.33

The cost therefore, of producing bait in 1958 was $0.76 per pound when based on the total estimated production of 470 buckets and an expense of $2,511.33, or $5.34 per 7-pound bucket.

As mentioned before, there is no allowance in these figures for the salary of the biologist in charge of the plant. If we assume that the plant could be operated on a commercial basis with one man working half time at a salary of approximately $2,000 per year, the total cost would be $4,511.33 and the cost of producing bait would be $9.59 per 7-pound bucket, or $1.37 per pound. These costs are reasonable, but we must consider the fact that most of the concrete structure of the hatchery was already in and that building a new hatchery would have increased the costs much more.

As mentioned before, the skipjack fishermen expressed high approval of the effectiveness of tilapia in catching the larger skipjack. In fishing for these larger skipjack the fishermen preferred using tilapia 5 to 6 cm. (2.0 to 2.4 in.) in length. Young tilapia between 3.8 and 6.4 cm. (1.5 and 2.5 in.) are generally suitable, however, as skipjack bait. A 3.8-cm. fish weighs 1.0 g., whereas a 5.1-cm. (2 in.) fish weighs 2.5 g., and a 6.4-cm. fish weighs 4.4 g. The bait fish delivered by the Paia plant in 1958 averaged 1.59 g. in weight and approximately 4.4 cm. (1.7 in.) in length. Whether tilapia are harvested at 4.4 cm. with approximately 2,285 fish to the bucket, or at 5.1 cm.

with 1,274 per bucket, is an important consideration in calculating the commercial feasibility of such a bait-rearing project. If the growth rate could be increased, the fishermen's preference for the larger size would have less importance to the producer—the cost of holding the fish to the larger size being compensated for by the more rapid rate of growth.

1959 OPERATIONS

The major expenses, not including the salary of the biologist, incurred at the Paia plant in 1959 are listed below.

In addition to the operating expenses incurred in 1959, it was necessary to supply feed and water for approximately 1 month in 1960 to the young fish that were held over in order for them to reach bait size.

Capital improvements: [1]	
Acclimatization tank	$600.00
Filter tank	300.00
Total	900.00
Operating expenses:	
1959:	
Feed—for adult fish	158.57
Feed—for young fish	446.18
Water	786.00
Electricity	417.04
Maintenance and care of grounds	150.00
Annual lease on plant area	240.00
Hauling bait fish to docksite	90.00
Subtotal	2,287.79
1960:	
Feed—for young fish	$60.00
Water	60.00
Hauling bait fish to docksite	100.00
Subtotal	220.00
Total	2,507.79

[1] Borne by Maui Fisheries and Marine Products, Ltd.

It would seem logical to amortize the cost of capital improvements in 1959 over a 10-year period and to charge a 6-percent interest rate on the total capital investment, which is now $5,253.24.

Total costs:	
Capital improvements	$525.32
Interest	315.19
Operating expenses, 1959	2,287.79
Operating expenses, 1960	220.00
Total	3,348.30

The cost of producing bait in 1959 was $1.01 per pound, or $7.06 per 7-pound bucket, when based on the total estimated production of 474 buckets and expenses of $3,348.30. The higher production cost per pound of bait in 1959 than in 1958 was due principally to greater expenditures for water, electricity, and feed.

If we assume that the plant could be operated on a commercial basis with one man working half time at an annual salary of approximately $2,000, the cost of producing bait-size fish then becomes $11.28 per bucket, or $1.61 per pound.

The 2-year operation of the Paia plant was successful with respect to the number of young fish produced per female. It was not judged economically successful, however, principally because the plant was too small. It is our belief that a plant designed on a commercial scale for volume production and with more efficient use of labor could be operated profitably.

APPLICATION OF RESULTS

ESTIMATED COMMERCIAL PRODUCTION COSTS

It is hazardous to project these preliminary data, but it is our opinion that a commercial plant much larger than the Paia hatchery could produce bait-size tilapia at a cost of about $1.00 a pound, which should bring the price of bait within the reach of tuna fishermen.

This projection is based on a plant with 16,000 square feet of brood-tank space and 40,000 square feet of fry-tank space, which is the size of plant that the Hawaii Division of Fish and Game plans to build with an appropriation of $130,000 granted for the purpose by the 30th Territorial Legislature. Such a hatchery could be stocked with 12,000 females and 4,000 males. Using the best production figures from the Paia hatchery, an average of about 1,000 young per female per year obtained in 1959, the total annual production should be about 12,000,000 young. If the fish were delivered as bait at a size when 2,000 constitute a 7-pound bucket, the hatchery should produce 6,000 buckets of bait annually. If the capital improvements were amortized over a period of 10 years, they would be prorated at $13,000 per year.

Operation of the plant would require 2 men working full time, at a cost of about $10,000 a

year for salaries. This estimated labor cost is higher than the estimate given for the Paia hatchery because of the larger scope of the operation. Feed would cost approximately $15,000 annually. Utilities, mostly electricity and water, would cost about $3,000 a year. Another $1,000 would be needed for miscellaneous equipment and for bait-hauling expenses. The annual operating cost would thus be approximately $29,000, with an additional $13,000 for capital improvements, or a total of $42,000. With the anticipated production of 6,000 buckets of bait, the cost per bucket would be $7.00, or $1.00 per pound. Land costs are not included in our estimates since the planned location of the hatchery is on State-owned land.

Brock and Takata (1955) estimated that the break-even value of nehu to the Hawaiian skipjack fishermen was roughly $4.23 per pound at the peak of the season. Therefore, if the cost of commercially produced bait were higher than $4.23, the fishermen would fare better by catching their own bait; and if the cost of a substitute bait were lower they would be better off to buy their bait.

ESTIMATED VALUE TO FISHERMEN

From the estimates of bait-production costs given in the previous section,we can estimate the potential value of tilapia to the commercial tuna fisherman. Hawaiian skipjack vessels ordinarily use 20 to 30 buckets of bait per trip when natural bait is in good supply. Let us assume that a boat purchases 30 buckets of tilapia at a cost of $7.00 a bucket and in 1-day's fishing catches 10,000 pounds of skipjack (as calculated from our average conversion rate in 1958 and 1959) worth $1,000 to the fishermen. If we deduct $210 for the cost of the bait, $15 for the crew's food, $25 for fuel and ice, for a total of $250, we have $750 remaining. The crew's share, or 63 percent, equals $472.50 for the day's operation. Based on an average crew per vessel of 10 men, the day's share for each crew member is $47.25.

We do not visualize that tilapia or any artificial bait substitute will entirely replace the nehu in the Hawaiian skipjack fishery. King and Wilson (1957) have estimated, however, that if the average fishing time for a sampan could be increased from the present 15 days a month to a possible 20 days a month through the use of tilapia or other supplemental bait, the total annual skipjack catch for Hawaii might be increased by 3 million to 4 million pounds. It is probable that the number of fishing days could be increased to well over 25 days a month if the entire bait needs or sufficient supplemental bait were supplied by a large tilapia hatchery. Such an increase in days fished in a month might conceivably increase the total annual skipjack landings for Hawaii by more than 6 million pounds.

CONCLUSIONS AND RECOMMENDATIONS

Location of the Plant

The site was characterized by strong, gusty winds, above average rainfall for the island of Maui, and a high rate of cloud cover. Although the wind aided in circulating the water, it also brought large quantities of dust and debris into the tanks. We concluded that a sheltered area on the drier and warmer leeward side of the island would have provided a more favorable site.

Arrangement of the Plant

The general arrangement was satisfactory but could have been improved in a few respects.

a. Both brood tanks should have been equipped with drains on their upwind end where the detritus collected. (The drains were installed in 1959.)

b. Aeration during the hours of darkness would help keep the oxygen level fairly high. (An aeration system was in operation in 1959.)

c. Fry tanks should have been built with a sump or catch basin to facilitate removal of fry. Considerable time was expended in seining the fish from the tanks, which were difficult to drain.

d. The plant had a ratio of brood-tank area to fry-tank area of 1 : 3.8. A ratio of 1 : 5 would have permitted less crowded conditions within the fry tanks and probably would have induced faster growth in the young fish.

Fish Feed

a. Fish 2 to 3 weeks of age fed well on a middlings–fish meal mixture and Purina starter feed; between 4 weeks and 3 months of age they readily accepted the Purina fry feed and always seemed to be hungry even with three feedings a day. At all ages, they fed on the algae in the tanks.

b. The particle size of the Purina small fingerling feed seemed to be too large for the 2- to 3-month-old tilapia.

c. The adults preferred Purina trout chow (developer), but appeared to remain in satisfactory condition on a millrun–fish meal mixture (4:1

ratio), or on rabbit ration. The adults fed extensively on the filamentous algae growing on the tank walls.

Fry Growth

a. Each of the fry tanks, which had an area of 71.5 sq. ft., yielded about 3 buckets of bait-size fish in 10–12 weeks when stocked with 5,000 to 7,000 fry.

b. We predict that by providing more space per fish, bait-size fish could be produced in 8 weeks.

Production Costs

a. In the first year of operation (1958), the Paia plant produced approximately 470 buckets of bait-size tilapia at a cost of $0.76 per pound, not including the salary of the supervising scientist. If the plant had been operated on a commercial basis, employing one caretaker half-time, we estimate that the total production cost including labor would have been $1.37 per pound.

b. In the second year of operation (1959), the Paia plant produced approximately 474 buckets of bait-size tilapia at a cost of $1.01 per pound, not including the salary of the supervising scientist. If the plant had been operated on a commercial scale, employing one caretaker half-time, we estimate that the total cost including labor would have been $1.61 per pound. The higher average cost in 1959 was due to larger expenditures for water, electricity, and fish food than in 1958.

c. Better plant design with a proportionately greater amount of fry-tank space would have resulted, we believe, in faster growth of the young fish and, therefore, lower production costs.

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APPENDIX

POND CULTURE OF TILAPIA

In 1956 and 1957, personnel of Hawaiian Tuna Packers, Ltd., and of the Bureau of Commercial Fisheries seined bait-size tilapia from two ponds adjacent to Honolulu and used the fish in experimental live-bait fishing for skipjack. One of the ponds, Kuliouou Pond, is a naturally occurring body of brackish water; the other, Ewa Pond No. 6, is an artificially created body of fresh water.

The number of adult tilapia in each pond was estimated from the frequency of capture of finclipped fish (appendix table 1). The quantity of young fish removed from each location in relation to the number of adults and size of the area provide some comparison with the production obtained in the brood tanks at the Paia, Maui, hatchery.

The natural food supply of the tilapia was supplemented in each pond during the study period by a daily feeding of rice bran.

Kuliouou Pond

This brackish-water pond is about 3 acres in extent and has a salinity of about 20 °/₀₀. King and Wilson (1957) obtained 105 pounds of bait-size tilapia from this pond on one seining trip in 1956. In 1957 a more detailed study of the pond was initiated to obtain an estimate of the size of the brood stock and the extent of production of young fish. Appendix table 1 gives the population estimates and summary of the fish removed.

Kuliouou Pond failed to yield any bait-size tilapia in four seining trips in 1957. The catch made on three of these trips is shown in appendix table 1. The adult population, estimated at the end of the experiment, was about 1,400 pounds. On each occasion, nests were observed on the bottom of the pond and evidence of spawning (females carrying ova or young in the mouth) was noted. The pond contained a large number of predators, which with the cannibalistic traits of the tilapia, practically eliminated all young fish.

Ewa Pond No. 6

This fresh-water pond, with few predators other than crayfish, was a much better source of bait-size tilapia. During 1956, King and Wilson (1957) obtained 436 pounds of bait-size tilapia in five seining trips to this pond. Nine seining trips in 1957 yielded 882 pounds of bait-size fish. The catch obtained on six of these trips is given in appendix table 1. The average catch of bait per trip was slightly higher in 1957 than in 1956.

Using the mark (fin clipping) and recovery method, the adult tilapia population in Ewa Pond No. 6 was estimated to be about 6,000 pounds when sampled in April and again in July 1957. The annual production of bait-size fish was, therefore, approximately 147 pounds per 1,000 pounds of adults. In the Paia, Maui, hatchery (this report) a brood stock weighing about 800 pounds produced about 3,300 pounds of bait-size fish per year, or 4,125 pounds of bait per 1,000 pounds of adults.

Although the adult tilapia population in this pond was fed rice bran daily, cannibalism probably reduced the amount of bait available. As reported by King and Wilson (1957), it was difficult to harvest the crop of young fish. Seining requires a rather large crew and is not efficient because of the tendency of the fish to burrow in the mud or hide in the spawning beds. Therefore, we believe that, in all respects, the large-scale production of bait-size tilapia is more practicable by the tank-culture method than by the uncontrolled pond-culture method.

APPENDIX TABLE 1.—*Seining results and population estimates, Kuliouou and Ewa Ponds, 1957*

Item	Kuliouou Pond			Ewa Pond No. 6					
	Mar. 26	May 1	July 10	Mar. 1	Mar. 8	Apr. 18	May 10	July 11	July 12
Number of hauls	10	10	6	1	1	2	5	4	4
Bait-size fish caught (lb.)[1]				6		83	56	106	107
Small to medium fish:[2]									
Caught and removed (lb.)	129	347.5	414	27	81				
Caught and returned (lb.)					138	188			126
Unmarked large fish:[3]									
Caught and removed (lb.)				741	[4] 1,184	300	308	38	177
Caught and returned (lb.)		62.5	66.5	[5] 1,202		412			355
Recovery and return of marked medium and large fish:[6]									
Number of males	18	50	43	124	408	502	(7)	(7)	189
Number of females	15	167	113	95	738	268	(7)	(7)	148
Total weight (lb.)	7	48	49.5	48	296	226			159
Estimated adult population (lb.)	[8] 1,081	1,360	1,384	9,188	7,781	5,910			6,189
Total, less adults removed (lb.)				8,447	6,597	5,610			6,012
95-percent confidence limits:[9]									
l_1 (lb.)	305	1,115	1,115	6,703	7,029	5,287			5,417
l_2 (lb.)	1,440	1,790	1,737	12,172	8,634	6,634			7,109

[1] Less than 3 inches long.
[2] 3 to 8 inches long.
[3] Greater than 8 inches.
[4] Large females, totaling 464 pounds, were marked and transferred to the Kuliouou Pond from this haul.
[5] Captured unmarked; marked and returned.
[6] Greater than 6 inches.
[7] Catch not examined for marked fish.
[8] Including 464 pounds of fish (large females) added March 8 from Ewa Pond No. 6.
[9] Following Chapman (1948).

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TANK CULTURE OF TILAPIA

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Until about two decades ago, the cichlid fish *Tilapia mossambica* Peters had received only minor attention as a food and game fish in its native East African environment. No intensive cultivation of tilapia was carried on in Africa, and it was not until this fish mysteriously appeared in East Java in 1939 that anyone recognized that it possessed many of the desirable characteristics of a pondfish and that it was readily adaptable to culture (Atz, 1954). The potentialities of various species of *Tilapia* were demonstrated by W. H. Schuster before a gathering of inland fisheries experts held at Surabaja in 1939 (Vaas and Hofstede, 1952). Since that time, tilapia have been successfully introduced into many southeastern Asian countries where they have become an important source of protein food.

In recent years, many scientists in various parts of the world have studied the biology of tilapia and its culture in ponds and rice paddies. The work of Vaas and Hofstede (1952), Chen (1953), Panikkar and Tampi (1954), and Swingle (1960) is particularly noteworthy. Chimits (1955, 1957) has published excellent reviews of tilapia culture and his bibliographies bring together a wealth of information on these fishes. Baerends and Baerends-Van Roon (1950) should be mentioned for their contributions to knowledge of the behavior of the cichlids. Other sources of information on various aspects of tilapia culture and biology are Brock (1954), on spawning in salt water; Fish (1955) and Le Roux (1956), on feeding habits; and Lowe (1955), on fecundity. Brock and Takata (1955) and King and Wilson (1957) reported on use of young tilapia as supplementary tuna bait, and Hida et al. (1961) on the tank culture of bait-size tilapia.

Swingle (1957) was the first to recognize that species of *Tilapia* have potentialities as a freshwater game fish in the United States. Other investigators have found several of the many species of *Tilapia* to be suitable laboratory animals for many types of physiological research.

The decision to introduce *T. mossambica* to Hawaii was based primarily on two major considerations: the usefulness of the fish for clearing aquatic vegetation from irrigation ditches and canals and the possibility that the young could be used as bait fish in the Hawaiian skipjack fishery (Brock and Takata, 1955). Since its introduction to Hawaii in 1951, tilapia has received widespread attention and is now well established in many private and commercial ponds throughout the major Hawaiian islands.

The pole-and-line fishery for skipjack (*Katsuwonus pelamis*) is the largest commercial fishery in Hawaii. Descriptions of this fishery and the associated live-bait fishery have been published by June (1951), Brock and Takata (1955), and Yamashita (1958). All of these investigators cite the shortage of bait fish as the principal factor limiting production of this pole-and-line fishery.

Because of this critical demand for bait, attention was focused on tilapia as a possible supplement to natural bait supplies. Tester et al. (1954), experimenting with artificial materials (both edible and inedible) to attract tuna to the stern of a fishing vessel, reported generally negative or inconclusive results, which gave added impetus to the search for a suitable substitute live bait. In the summer of 1954, Brock and Takata (1955) initiated the first sea trials to evaluate tilapia as live bait and in a number of the sea tests they obtained encouraging results. King and Wilson (1957: p. 8) made further sea tests during the summer and fall of 1956 and concluded that the young of *Tilapia mossambica* are an adequate bait fish for catching skipjack. They further pointed out that although tilapia in some respects was in-

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ferior to nehu (*Stolephorus purpureus*), the principal bait used in the skipjack fishery, it was on the other hand, hardier than nehu and could tolerate a wider range of salinity and lower oxygen concentrations.

In view of the reported success in using young tilapia as a tuna bait fish, consideration was given to devising rearing methods that would be economically and biologically feasible for producing adequate numbers of fish of proper size. Two immediate possibilities presented themselves: pond culture, whereby existing ponds on the islands would be utilized with some modifications; and tank culture, with separate spawning tanks and fry-rearing or nursery facilities.

King and Wilson (1957: p. 8) utilized bait-size tilapia obtained from private ponds and reservoirs for their sea trials and after a number of bait-seining operations concluded that—

> it does not appear that the rearing of tilapia for bait purposes can be done most effectively in water reservoirs and natural ponds with little control over spawning, cannibalistic traits of the species, and predation, and with the difficulty of harvesting the fish efficiently at an optimum size.

It was anticipated that tank culture of the fish under controlled conditions might prove to be a more efficient and economical way to produce bait-size tilapia. As a result, a study of tank culture of tilapia on a pilot-plant scale was initiated at the Bureau of Commercial Fisheries Biological Laboratory at Honolulu. The primary objectives of this study were to determine the physical and biological problems associated with tank culture and the potentialities of producing bait-size tilapia in sufficient quantities under controlled conditions in a hatchery-type operation.

The pilot plant was constructed on the grounds of the laboratory in October 1956 and experiments were carried on there until July 1958, after which the facilities were transferred to more spacious grounds adjacent to the laboratory's new docksite building at Kewalo Basin, Honolulu. Studies continued at the Kewalo plant until September 1959. While the purpose of the pilot plant was primarily to examine the general problems associated with production of bait-size tilapia, the Kewalo plant studies were designed to obtain a more detailed and quantitative evaluation of tank culture and to assess the various factors associated with variations in reproductive, survival, and growth rates.

The purposes of this report are to discuss our efforts in establishing operational procedures and basic requirements that would be applicable to a commercially operated tilapia hatchery, to present our observations and conclusions on reproduction and growth, and to describe the cannibalism, predation, and diseases of tilapia observed during the experiments.

As work progressed, the need for information on other rearing methods became evident and a study of pond culture of tilapia under controlled conditions was begun by the Hawaii Division of Fish and Game at Kaneohe, Oahu, under contract with the (Territorial) Economic Planning and Coordination Authority (EPCA) and the Bureau of Commercial Fisheries. Production of bait-size tilapia in ponds under uncontrolled conditions was investigated to some extent by King and Wilson (1957) during the summer of 1956.

The Maui Fisheries and Marine Products Co., Ltd., expressed an interest in establishing a tilapia hatchery on a semicommercial basis, following our initial success in producing bait-size tilapia at the pilot plant. A contract was signed with Maui Fisheries, the Hawaii Division of Fish and Game, and the Bureau of Commercial Fisheries, as principals, late in December 1957, for the operation of a tilapia-rearing plant at Paia, Maui. A fishery biologist, supplied by the Bureau, was placed in charge of the plant to obtain detailed records of the production and of operational costs. The Paia hatchery was operated for 2 years and the results have been reported by Hida et al. (1961).

In frequent references throughout this report to the various stages of development of tilapia, we have tried to conform to generally accepted terminology, but in some instances we found combinations of categories more suitable and in other ways we have diverged from ordinary usage. The terminology that we have employed is defined as follows:

Fry.—Includes both the prolarval (yolk-bearing) and postlarval (nonyolk-bearing) stages. Includes tilapia up to 19.0 mm. (0.75 in.) in length.

Juvenile.—Stages between fry and adult, with a range in size from about 20 to 100 mm. (0.75 to 4 in.).

Bait size.—Juveniles suitable for skipjack bait range in size from about 38 to 51 mm. (1.5 to 2 in.); however, on several occasions juveniles falling outside this length range have been used for bait.

Young.—A general category that includes fry and juveniles.

Adult.—Mature fish that are potential breeders and are distinguished by the display of coloration, especially by the males in the reproductive phase. Larger than 100 mm. (4 in.) in length.

The length measurement used in this report is fork length; that is, the length from tip of the snout to ends of the middle caudal rays. Body measurements (length and weight) were made in both English and metric units during the early phases of the investigation. However, all original measurements in English units have been converted to their equivalent in metric units, and where applicable or when appropriate the English units are given in parentheses. Reference to plant facilities is either to the pilot plant constructed on the grounds of the Bureau's Honolulu Laboratory or to the Kewalo plant located at the Kewalo Basin docksite.

We gratefully acknowledge the advice and suggestions given us by the Bait-fish Research Coordinating Committee composed of biologists of the Hawaii Division of Fish and Game, the University of Hawaii, and the Bureau of Commercial Fisheries, Honolulu, and representatives of the Hawaiian Tuna Boat Owners Association and the Hawaiian Tuna Packers, Ltd.

CULTURE METHODS

REARING FACILITIES

Pilot Plant

Three redwood raceway-type tanks, each 5 feet wide by 20 feet long and 3 feet deep, with a capacity of 1,400 gallons, were constructed on the grounds of the laboratory in October 1956 (fig. 1). The floors sloped downward toward the outflow end of the tank at the rate of 1 inch for each 10 feet of length. The outflow, located in one corner of the tank, consisted of a removable standpipe that slipped into a hole in the floor of the tank and connected with a gate valve and drainpipe on the outside. Baffle boards and a brass screen enclosed a triangular area occupied by the standpipe. The baffle boards were raised about

FIGURE 1.—A redwood raceway tank at the pilot plant.

2 inches above the floor. Thus, the outflowing water was drawn from the floor of the tank and aided in removing detritus from the tanks. The brass screen prevented the fry from being carried out through the drain. The inflow, situated on the opposite end of the tank, was a faucet from which fresh water from the Honolulu water supply was dripped into the tank at the rate of one-half to 1 gallon a minute. The tanks were given a coat of aluminum paint before being used.

Initially, these three tanks were used as brood or spawning tanks. With the onset of fry production in December 1956, it was necessary to convert one of the tanks to a fry-rearing tank. Continued fry production created a need for more rearing space. In June 1957, a fourth redwood raceway-type tank, 30 inches wide by 30 feet long and 30 inches deep, with a capacity of about 1,250 gallons, was constructed adjacent to the other tanks. Screens of fine-meshed Monel stretched over square wooden frames were used to partition the tank into six approximately equal compartments. Each compartment had a siphon-type drain of plastic tubing. A standpipe drain was placed at one end of the tank in the event that the

siphons clogged or failed. Each compartment was served by a fresh-water tap.

In June 1957 we acquired a number of surplus assault boats from the U.S. Army, four of which were installed at the laboratory and used as brood and fry-rearing tanks. These undecked plywood boats measured approximately 4 by 12 feet on the bottom and each had a capacity of about 840 gallons. Although of very light construction, they were fairly watertight for more than a year. Water flowed in through a hose attached to the stern; the drain consisted of a plastic siphon attached to the bow. Several 1-inch holes were drilled in one side of the square bow just above the water line for controlled overflow if the siphon failed. Figure 2 shows an assault boat converted into a fish-holding tank, while figure 3 illustrates the plan of the pilot plant.

A filter system, consisting of a sand filter box and a pump, was installed experimentally on tank 2. It soon became apparent that the filter box was not adequate and that beach sand was inappropriate as a filtering medium. Cleaning and backflushing of the filter was necessary two or three times a week, requiring considerable time and effort. The sand was eventually replaced with several layers of fine-meshed Monel screen, which was not a very effective filter but did remove large amounts of fecal matter and other detritus. The turbulence and the splash on the surface caused by the water as it was returned to the tank under pressure also increased the oxygen concentration.

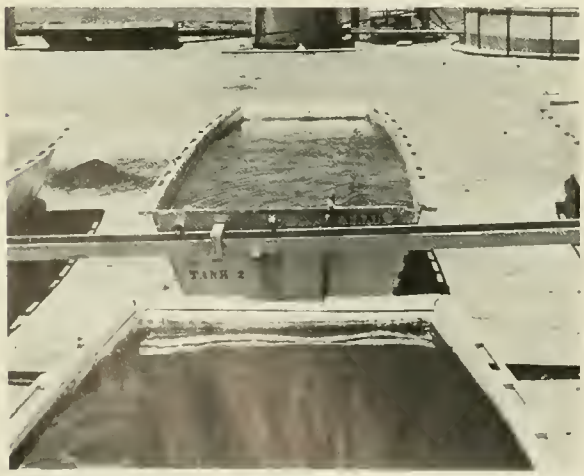

FIGURE 2.—An assault boat converted into a fish-holding tank, Kewalo plant.

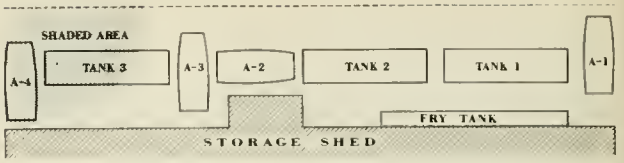

FIGURE 3.—Plan of the tilapia pilot plant.

Other minor modifications in the pilot plant included installation of an aeration system and floodlights on tank 3. The aeration system consisted of an air compressor, a rubber air hose, and a pipe (drilled with holes) that ran crosswise of the floor in the center of the tank. Air was pumped through this pipe and slowly bubbled through the water in the tank.

Two 150-watt projector floodlights were installed on tank 3, one at each end, approximately 5 feet above the surface of the water. It was hoped, by day-and-night illumination, to increase the algal content of the tank, which was very low, and also possibly increase the production of young. No changes were detected, however, and the floodlights were removed after 3 months.

Kewalo Plant

In July 1958, the redwood tanks (three brood tanks and one fry tank) at the pilot plant were dismantled and reassembled at the Kewalo Basin docksite. A filter system (fig. 4), consisting of a sand filter box 24 inches wide by 26 inches long and 18 inches deep and a pump, was attached to each of the three brood tanks. The fry tank was modified by increasing the width 10 inches and by partitioning it with plywood separators (instead of screens) into six compartments. Essentially, each compartment was a separate tank with its own drain and tap. A filter box, 30 inches on the sides and 18 inches deep, and a pump were installed to filter and to recirculate the water.

The four assault-boat tanks at the pilot plant, after being in use for about a year, were not worth salvaging. Thirteen assault boats were removed from storage and converted into 12 brood tanks and 1 filter tank at the Kewalo plant. Drain water from the tanks was carried down a flume to the sand-filter tank and pumped back to each tank. All filter boxes contained a bottom layer of crushed rock and a top layer of coarse black sand (volcanic cinders), which was found to be much more effective than the fine beach sand used initially.

FIGURE 4.—Filter and pump on a raceway tank.

The general arrangement of the assault-boat tanks and the redwood tanks is shown in figure 5.

STOCKING THE BROOD TANKS

One of the first problems to be considered in the operation of the pilot plant was what sex ratio should be used when stocking the tanks. Chen (1953: p. 6), working on tilapia in Taiwan, stated that the proper sex ratio for propagation purposes is one male to a female. Other investigators, however, reported that in mouth brooders, which group includes *T. mossambica*, the female visits the spawning grounds only briefly to extrude her ova and collect the fertilized eggs, and then moves away or often is chased away by the male. The male remains on the spawning ground to guard the nest and immediately begins to court other females. He is, thus, available for and presumably capable of fertilizing ova from a succession of ripe females (Baerends and Baerends-Van Roon, 1950; Lowe, 1955). Lowe (p. 48), with respect to the mouth brooders, concluded that as male fish can continue fertilizing over a long period, the number of eggs ferti-

FIGURE 5.—Tilapia tanks at the Kewalo plant after a heavy rain.

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lized appears to be determined more by the number of ripe females than by the number of males.

Taking advantage of this behavior to realize a maximum production of young with a minimum of brood stock, a ratio of 2 ♀ : 1 ♂ was tried initially, with results that were considered to be successful. A later experiment at the pilot plant using a ratio of 5 ♀ : 1 ♂ yielded less-successful results, as will be described later.

Another important consideration was the density of the brood stock or carrying capacity of the brood tanks. Originally, it was decided to try a total of 48 fish with about 1.9 square feet per individual in one tank, and 96 fish or approximately 0.9 square foot per individual in the other two tanks, each with a sex ratio of 2 ♀ : 1 ♂ (table 1).

TABLE 1.—*Number of adults of each sex and space allowance per male and per individual, in brood tanks at the pilot plant*

Tank No.	Number of males	Number of females	Bottom area (sq. ft.) per—		Volume of water per individual (cu. ft.)
			Male	Individual	
1	32	64	2.8	0.9	1.9
2	32	64	2.8	.9	1.9
3	16	32	5.6	1.9	3.8

On October 12, 1956, the three tanks at the pilot plant were stocked with adult fish averaging 20 cm. (8 in.) in length and 150 g. (5.3 oz.) in weight. These fish were supplied by Hawaiian Tuna Packers, Ltd., and obtained from Ewa plantation pond No. 6. The initial mortality among the brood stock was very low, amounting to only three males and three females the first 15 days after stocking. All casualties were replaced. The exact number of adult fish in each of the tanks varied during the course of the test, however, owing to unobserved mortalities, vandalism, and the recruitment of juveniles that escaped dipnetting and grew to adult size in the brood tanks.

The stocking of the Kewalo plant followed an experimental design and will be discussed under factors affecting reproduction, page 37. Stock for the Kewalo plant was also obtained from Ewa pond No. 6. The males averaged 142 g. (5 oz.) and the females about 113 g. (4 oz.) in weight. No length measurements were made.

FEEDING

Many investigators have reported on the feeding habits of the various species of tilapia. Generally, *T. mossambica* is considered to be omnivorous (Schuster, 1952; Chen, 1953; Atz, 1954; Panikkar and Tampi, 1954; Brock and Takata, 1955; Van Pel, 1955). Vaas and Hofstede (1952: p. 35) stated that tilapia is herbivorous, but will feed on planktonic Crustacea "if such kind of food is more plentiful than vegetable food" and will show a preference for vegetable food when a mixture of the two is present.

Feeding of the brood stock at the pilot plant was started immediately after stocking was completed. Various types of commercial feed, such as rice bran (powdered), millrun (powdered), chicken starter mash (powdered and granules), alfalfa pellets ($^9/_{32}$ in. in diameter), pelletized rabbit feed ($^5/_{32}$ in. in diameter), and a pelletized pond-fish feed ($^5/_{32}$ in. in diameter), were tried to determine which were most acceptable to the fish. With a daily feeding rate of about 2 percent of the fish weight, we observed that finely divided, unpelletized feed, such as rice bran, millrun, and chicken mash, was not efficiently utilized because of the small particle size. The leftover feed contributed to fouling of the tanks. The alfalfa pellets and rabbit feed were also found to be undesirable because of their high content of indigestible fiber, which collected on the bottom of the tanks and also caused fouling.

Early observations on the feeding habits of the newly emerged fry indicated that they did not respond to supplementary feed until about 2 weeks after they were placed in the fry tank. The fry grade of pondfish feed (granules) was further ground to a flourlike consistency to accommodate the very young. The larger fry and juveniles reared at the pilot plant were fed pondfish feed in the crumble grade, which was slightly larger than the fry-grade granules.

Except in feeding experiments, the brood stock at the Kewalo plant was fed almost exclusively on a prepared trout feed (developer grade, about $^1/_4$ in. in diameter), which in a smaller particle size was also fed to the fry (starter grade, powdered; fry grade, granules) and juveniles (small fingerling grade, crumbles). Table 2 gives the composition, supplied by the manufacturer, of the various feeds that were used.

TABLE 2.—*Guaranteed analyses (percent) of ingredients in the feeds used at the pilot plant and the Kewalo plant*

Feed	Protein [1]	Fat [1]	Fiber [2]	Ash [2]	Added minerals [2]	Nitrogen-free extract [1]	Moisture [2]
Rice bran	9.0						
Chicken mash	20.0	4.0	4.5	7.5			
Alfalfa pellets	15.0	2.0	28.0	12.0		35.0	
Pondfish feed	30.0	4.5	6.0			28.0	
Trout feed:							
Developer	25.0	4.0	3.5			44.0	
Starter, fry, and small fingerling	40.0	2.5	5.5	9.0		44.0	12.0
Wheat white middlings	13.5	3.0	4.0	5.0			13.0
Millrun	12.0	3.0	10.0	6.0			14.0
Rabbit feed	16.0	2.5	21.0	10.0	3.0		

[1] Not less than.
[2] Not more than.

The brood stock at both plants was fed once a day, usually at midday. There were periods during the operation of both plants when the adults did not feed readily, and during these times smaller portions were supplied to the fish. This apparent lack of interest in feeding is probably associated with the mouth-brooding habit of the female.

The amounts of the various kinds of feed that were supplied to the adults and young during operation of the pilot plant and the Kewalo plant are given in tables 3 and 4. The fry were usually fed twice a day during weekdays, once in the morning and once just after midday, and once a day on weekends. The amount of feed given to the young varied with the number and size of fry and juveniles.

TABLE 3.—*Amount (in pounds) of the feeds used at the pilot plant*

Month	Rice bran	Chicken mash	Pondfish feed		Alfalfa		Rabbit feed
			Pellets	Crumbles	Pellets	Meal	
1956:							
October	2.5	2.5	25.0				
November		8.8	50.8				
December	22.0	16.0					
1957:							
January	23.3		11.0	3.5			
February			26.0	8.9			
March			31.0	11.6			
April			30.0	12.2			
May			31.0	15.0			
June			31.5	18.9			
July			30.0	19.6			
August		8.0	30.0	13.1			
September		15.2	30.0	14.8			
October		14.0	31.5	21.5	1.0	0.8	
November			36.8	14.0	7.2	7.0	
December			46.0	11.4	7.8	3.6	
1958:							
January			50.0	0.1	0.5		
February			38.5	0.1			
March			42.6	4.8			
April			40.4	6.0			
May			1.4	3.5			44.2
June				2.3			45.0
July				1.2			25.0
Number of pounds	47.8	64.5	613.5	182.5	16.5	11.4	114.2
Average cost per pound	$0.04	$0.05	$0.17	$0.27	$0.04	$0.04	$0.06

TABLE 4.—*Amount (in pounds) of the feeds used at the Kewalo plant*

Month	Trout feed		Rabbit feed	Millrun	Wheat white middlings
	Developer	Fry and small fingerling			
1958:					
August	57.1		7.0	7.0	
September	111.6	0.2	14.8	14.8	
October	107.6	1.6	14.0	14.0	
November	93.1	2.5	13.0	13.0	
December		1.5			
1959:					
January	40.5	1.7			
February	42.0	1.7			
March	44.2	1.7	2.2		
April	22.5	5.2	22.5		
May	46.5	9.7			0.4
June	45.0	20.8			1.6
July	51.2	21.2			5.3
August	68.5	22.4			3.1
September	22.0	29.5			
Number of pounds	751.8	119.7	73.5	48.8	10.4
Average cost per pound	$0.13	$0.13	$0.06	$0.04	$0.05

FRY PRODUCTION

T. mossambica reportedly first spawns at the age of 2 to 3 months and at a length of 8 to 9 centimeters. The frequency of spawning varies considerably, depending on environmental factors, and ranges from 6 to 16 times a year (Chen, 1953; Panikkar and Tampi, 1954; Chimits, 1955). Chen reported that a spawning fish of about 8 cm. in length produces from 100 to 150 ova at each spawning, although at the first spawning it may produce less than 100 ova. He stated further that the number of ova spawned increases with successive spawnings, so that a fish more than 6 months of age may produce in excess of 1,000 ova per spawning.

The developmental period of the ova is likewise variable but, generally, the ova hatch after 2 to 5 days and the young are carried in the mouth of the female for another 5 to 8 days before they are released (Chen, 1953; Panikkar and Tampi, 1954; Chimits, 1955).

From the time of the initial stocking at the pilot plant, careful daily observations were made on each tank to determine if young were being produced. As no signs of young fish were seen for about 6 weeks, the three tanks were partially drained and cleaned on November 28–29, 1956. Before the water level was restored in each tank, the detritus on the bottom of the tank was ex-

amined for signs of ova and young. The females were also examined to see if ova or young were being carried in the mouth. It was noted at this time that all the brood stock appeared in excellent condition but there were no signs of spawning.

On December 5, 1956, one-half cubic yard of white beach sand was placed in two of the brood tanks (tanks 1 and 3), covering the bottom to a depth of about 3 inches. It was our original intention to determine if the tilapia would spawn on the bare floor of the tanks, which seemed probable in view of Chen's (1953: p. 7) observation that tilapia were seen spawning successfully in a garden pond with a concrete bottom.

Good evidence of excavating and nest-building was noted the next morning following placing of the sand, and the nests continued to increase in number during the next few days until they occupied at least two-thirds of the sandy bottom. Two weeks after the sand was placed in the tanks, the first young were noticed on the surface of tank 1. The young were removed and subsequently placed in tank 2, which was drained and converted into a fry tank. Six days later, the fish in tank 3 started to produce young.

During the draining of tank 2 in preparation for conversion into a fry tank, one large male was observed carrying six yolk-sac fry in its mouth cavity, although in this species the female is supposed to brood the young. This behavior was also observed by Vaas and Hofstede (1952), who reported that the male incubated the ova in exceptional cases. Further evidence of spawning was found in tank 2, where many ova and yolk-sac fry were seen widely scattered on the tank floor. It was our supposition that the adults had become excited as the water level dropped and ejected the ova and fry.

At the Kewalo plant, where all the brood tanks were supplied with sand, fry production started 11 days after the tanks were stocked. Further data on fry production at the Kewalo plant will be presented later in this report, together with the results of the various experiments.

FRY COLLECTION

Newly hatched fry of *T. mossambica* measure 5 millimeters in length, 5.8 mm. on the second day, and 8.0 mm. at the end of the fifth day. On about the fifth day, they begin to spend less time in the mouth of the female or leave it altogether and swim about in a tight school near the surface of the water, feeding on tiny food particles (Panikkar and Tampi, 1954). This behavior of the fry made their capture by dipnetting a relatively simple process. Another behavior pattern that became evident to us through daily observation was the tendency for the fry to congregate along the walls of the tank, especially in the corners and, at times, directly under the inflowing water.

At both plants, the young emerging each day were captured with a fine-meshed dipnet and counted as they were released into the fry tank. Although our daily netting effort varied somewhat in efficiency, as indicated by the different-sized young netted, the method proved to be quite effective as evidenced by the few juveniles that were removed from the tanks when they were drained.

Early in the operation of the pilot plant, the displacement and weight methods for assessing the daily production of young were considered, but both had major drawbacks for enumerating the very small tilapia fry. We concluded that only by an actual count could we obtain the accuracy desired.

In August 1957, a shelf-collection method of capturing young was investigated at the pilot plant. This method was originally the idea of biologists of the Hawaii Division of Fish and Game who observed that tilapia fry tended to congregate in shallow water near the edge of the ponds. Consequently, it was hypothesized that if the fry had shallow water available to them along the walls of the brood tank, perhaps their capture would be simplified.

A redwood shelf, running the length of the inside wall just below the waterline, was installed in tank 1. The water level in the tank was maintained so that the outer edge or lip of the shelf was ordinarily about one-half inch below the surface. The water over the shelf could be drained through a hole in the wall of the tank and the young fish caught in a net.

Comparison of the number of fry collected from the shelf with that collected elsewhere in the tank by dipnetting indicated that the shelf was effective in the removal of only about 25 percent of the fry that emerged daily. Further, many of the fry congregated under the shelf, rather than over it.

In view of the results that were obtained, the shelf collection method was abandoned.

FRY REARING

As fry production increased, it became a serious problem to provide sufficient space for the young fish. Initially, the fry were placed in one large fry tank. After a few weeks, cannibalism became widespread: the juveniles readily devoured the newly collected fry when they were transferred to the fry tank. As a remedy, removable frames covered with fine-meshed Monel screen were installed in the tank dividing it into three compartments. The fry and juveniles could then be segregated by age and size.

With the construction of a new fry tank with six compartments and the acquisition of four assault-boat tanks at the pilot plant, additional space for rearing the young was available. The procedure became standard to place the fry in the fry tank for about 4 to 5 weeks, after which time they were transferred to assault-boat tanks.

When fry were removed from the brood tanks, they usually ranged in size from 7.8 to 13.6 mm., with the average about 10.8 mm. Of a total of 154 fry ranging from 7.8 to 10.3 mm., about 26 percent carried remnants of the yolk sac. The newly collected fry, as mentioned earlier, generally paid little or no attention to the prepared feed when first offered it and only took it after about 2 weeks in the fry tank.

Vaas and Hofstede (1952) observed that young tilapia fed on diatoms, unicellular green algae, small Crustacea, and periphyton. Varying numbers of these organisms were present in the tanks and undoubtedly constituted a major portion of the diet of the fry during their first few weeks of life after absorption of the yolk sac. The feces of the young fry were usually bright green, indicating that algae were a major constituent of their diet.

The necessity of utilizing all fry-rearing space available during periods of heavy fry production occasionally forced us to overcrowd the fry tank and frequently resulted in an outbreak of disease. A criterion for determining when an overcrowded condition existed was difficult to formulate, but through experience we arrived at what we considered an optimum stocking density. The general plan was to stock the fry-tank compartments with approximately 200 fry per square foot of surface area and crop each compartment at frequent intervals, removing the larger, faster-growing individuals; i.e., fish that were 20 mm. (0.75 in.) or larger. In this manner, cannibalism and disease were kept to a minimum. Also, through the necessity of occasionally overcrowding the juveniles in the assault-boat tanks, we learned that they were much more tolerant to crowding than were the fry and also that they were afflicted less frequently with ectoparasites.

The most critical period for the fry appears to be the first 4 to 5 weeks of life, for it is in this period that the fry are most susceptible to infectious diseases and ectoparasitic infestation. Proper sanitary conditions in the tanks and adherence to an optimum stocking density for a given area seem to be the two most important factors determining survival and subsequent health of the fry.

LENGTH-WEIGHT RELATION OF YOUNG

During the operation of both plants, it was frequently necessary to estimate the size and quantity of young fish on hand. In order to have a convenient means of converting length into weight and vice versa, the length-weight relation for tilapia 17 to 73 mm. in length was determined from body measurements of 109 fish. The logarithmic formula for the expression of this relationship is

$$\log W = 3.088 \log L - 4.8935$$

where W is the weight in grams and L is the length in millimeters. A curve demonstrating the length-weight relation is shown in figure 6.

WATER-QUALITY DETERMINATIONS

Some chemical determinations were made routinely once each week. Only oxygen measurements were made at the pilot plant; but at the Kewalo plant, additional properties, such as free carbon dioxide, bicarbonates, normal carbonates, and hydrogen-ion concentration were also measured weekly in selected tanks.

Oxygen Content

Determinations of dissolved oxygen in the brood and fry tanks were made by the modified Winkler method. Analyses were made once a week at

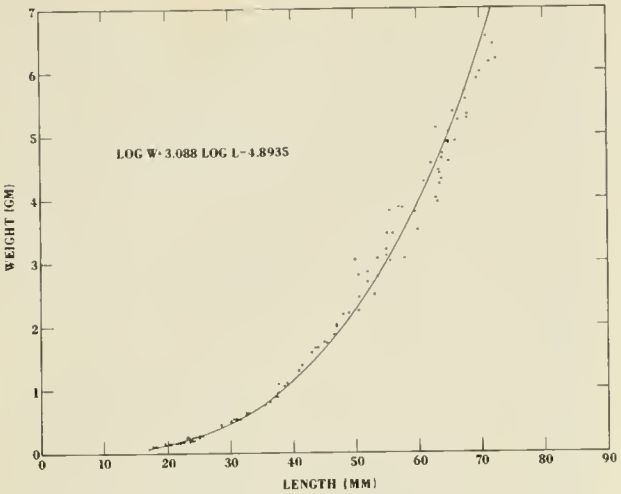

FIGURE 6.—Length-weight relation for tilapia 17 to 73 mm. in length.

about the same hour each time to obtain a general record of the variation in oxygen content of the water (appendix tables 1, 3, 4, and 5). In a 24-hour series (with sampling at hourly intervals) obtained at the pilot plant November 12–13, 1957, we found a marked diurnal change in the concentration of oxygen in the tanks, the minimum concentration occurring at about daybreak and the maximum concentration at about midafternoon (fig. 7; appendix table 2). The maximum concentration was certainly the result of photosynthesis by the algae in the tanks, and the minimum was caused by respiration of both algae and fish. Water temperatures in the tanks showed a similar diurnal variation, with the occurrence of maximum and minimum temperatures corresponding very closely to the maximum and minimum concentrations of oxygen.

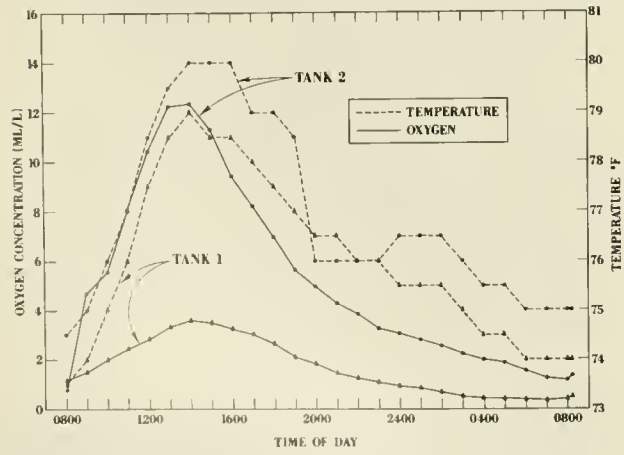

FIGURE 7.—Diurnal variation in oxygen concentration and temperature in tanks 1 and 2 at the pilot plant.

Vaas and Hofstede (1952) stated that *T. mossambica* has a high metabolic rate compared with carp, and that oxygen is consumed and carbon dioxide liberated in large quantities within a short time by the species. They also found that when oxygen tension is low, especially during the morning, the fish concentrate at the surface of the water suspended in a diagonal position, sucking in the well-aerated water of the surface layer with wide-open mouths.

It is suspected that some of the mortalities among the adults at both plants were associated with an insufficient amount of oxygen. In tank 3 at the pilot plant, deaths occurred periodically for about 2 months in the summer of 1958. During this period, the oxygen minima occurring in the early morning were consistently low, averaging only 0.38 ml./l. Of the 10 adults that died during this period, 9 were large males averaging 29 cm., and the single female was 23 cm., perhaps indicating the greater susceptibility of the larger tilapia to low oxygen concentration.

Since our purpose in sampling oxygen was primarily to monitor environmental suitability, we have not attempted to relate the data to fry production, except in the heating experiment, where low oxygen concentrations were believed to be associated with the poor fry production. From the data it appears that, in most instances, the minimum or near-minimum oxygen concentration in the sampled tanks was sufficient to sustain the tilapia.

Hydrogen-Ion Concentration

Determination of hydrogen-ion concentration was made by the colorimetric method at the time the oxygen samples were drawn. The pH values of the tanks that were sampled (appendix tables 6–8) ranged from 7.3 to values exceeding 8.8 (the color standard used at first could measure pH only to 8.8). It was expected that the pH in our tanks would remain on the alkaline side, since city water (pH range, 7.9 to 8.3) was used and, with the exception of the fry tank, the tanks contained a 3- to 4-inch layer of calcareous beach sand.

The hydrogen-ion concentration and its significance to aquatic organisms has been relegated for some time to a minor position by many investigators (Welch, 1935; Odum, 1959). It may possibly be a limiting factor to some organisms, however.

Free Carbon Dioxide

Analysis of the amount of free carbon dioxide in the tanks was started at the Kewalo plant in February 1959. The samples were drawn immediately after those for the oxygen determination had been drawn and fixed. The amount of free carbon dioxide present was approximated by titration of a 100-ml. sample to the phenolphthalein endpoint with 0.02 N sodium hydroxide.

Welch (1935: p. 175) stated that carbon dioxide is one of the most important substances in the life of organisms, but that it should be present only under suitable circumstances and in proper amounts. He stated further that a small amount of carbon dioxide appears to be essential for aquatic animals. Doudoroff (1957) regarded free carbon dioxide concentrations between 100 and 200 p.p.m. as fatal to moderately susceptible freshwater fishes; also, that exposure to concentrations between 50 and 100 p.p.m. causes immediate distress and may be lethal if the exposure is prolonged. He noted that even in polluted waters free carbon dioxide concentrations rarely exceed 20 p.p.m.

Throughout the period of sampling at the Kewalo plant, the free carbon dioxide concentration (appendix tables 9 and 10) was never found to be in excess of 16.2 p.p.m. No attempts were made to determine a relation between carbon dioxide concentrations and fry production. Our routine observations were made primarily to detect excessive amounts of free carbon dioxide in the brood and fry tanks.

Alkalinity

Chemical analyses of the water in the tanks at the Kewalo plant included determinations of total bicarbonate and carbonate alkalinity. A 100-ml. sample was titrated with 0.02 N sulfuric acid against the phenolphthalein and methyl orange endpoints.

Alkalinity directly influences the biological productivity of a body of water. The carbonates and bicarbonates, which are in close chemical combination with carbon dioxide, are utilized by algae (Welch, 1935), and also act as buffers by keeping the hydrogen-ion concentration close to the neutral point (Odum, 1959).

Our alkalinity determinations (appendix tables 8 and 10) were made primarily to gain a general knowledge of the type of water present in the tanks, as soft water has a smaller supply of these ions and, therefore, is less productive.

MORTALITIES

Among the Adults

Observed mortalities among the brood stock amounted to 31 males and 11 females at the pilot plant and 55 males and 56 females at the Kewalo plant. The dead fish were carefully examined and deaths were usually attributable to one of the following factors: Rough handling, disease, asphyxiation and, possibly, hydrogen sulfide poisoning.

While it might have been possible to reduce mortalities by using more care in handling fish and by proper treatment of diseased fish, it was not always possible to prevent mortalities caused by asphyxiation, since many factors contributed to the oxygen concentration in the tanks.

The heaviest mortality to occur in a single day among the adults was experienced at the Kewalo plant. A total of 7 males and 29 females was found dead in the two brood tanks containing brackish water (salinity-spawning experiment) and the deaths were believed to have been caused by either asphyxiation or hydrogen sulfide. Faint odors of hydrogen sulfide gas were detected in the brackish-water tanks for several days before the mortalities occurred, and, undoubtedly, this gas was one of the contributing factors, if not the determining factor in the deaths. The tanks were not drained and cleaned at the time hydrogen sulfide was first detected in the tanks, however, because the experiment was to be terminated within a few days.

Among the Young

Many factors contributed to the loss of young fish, chief of which was disease, with deaths from handling judged to be of secondary importance. At the pilot plant, the observed mortality in the fry tank amounted to 34,784 fish, while juvenile deaths totalled 4,523 fish. Although the total observed mortality among the young amounted to

15.5 percent of the 253,548 fish produced, the unobserved mortality (difference between net production and observed distribution and losses) was much higher, amounting to an estimated 42,900 fish or about 17 percent of the total production. The causes for these unobserved losses were difficult to assess, but presumably can be attributed to a variety of factors: vandals entering the plant and removing unknown quantities of fish; loss of fish through the drain; predation by dragonfly nymphs; and cannibalism. Davis (1946: p. 9) in reporting on "uncounted mortality" in trout hatcheries stated that this was due "either to improper construction of the raceways, so that many of the fish are able to escape; to the attacks of enemies, such as fish-eating birds; or to cannibalism."

At the Kewalo plant, observed mortalities among the young amounted to 44,600 fish or about 13 percent of the 347,700 fish produced.

DISEASE PREVENTION AND CONTROL

Prevention and control of fish diseases and infestation of parasites are important factors in the success of any type of fish-rearing program. Fish, like other animals, are subject to a wide variety of infectious diseases and parasites and seem particularly susceptible in an unnatural or artificial environment.

Several outbreaks of disease or parasitic infestation were observed among tilapia at both the pilot plant and the Kewalo plant. All dead fish were examined microscopically for signs of unnatural conditions, such as mucous film or irregular blotches on the body and unusual blisters or swelling. When sick fish were observed in the tanks, similar examinations were made on their external surfaces, gill region and, on occasion, the gastrointestinal tract. It was not always possible to distinguish between losses from diseases and from other causes, although in many instances of high mortality rates parasites were seen and identified to genus. Several exceptions occurred when the cause of high mortality rates among the fry could not be determined by isolation of any causative organism. By careful observation of symptoms, it was possible on a few occasions to restrict the probable cause of death to a virus infection. In general, the fry, juveniles, and adults were susceptible to infection in that order.

Trichodina spp.

Infestation by the ectoparastic trichodinids, considered one of the most highly specialized protozoans, was the most common malady among adult and young tilapia, with infestation along the dorsal fins, dorsal region of the caudal peduncle, and gill region being most prevalent. Tilapia with trichodiniasis were sluggish, showed loss of appetite, had a reddish tinge on the skin in the caudal-peduncle region, and, in some instances, in and around the region of the dorsal fins, they had white blotches accompanied by a fraying of these fins.

According to Davis (1953: p. 220), *Trichodina* is very easy to control. We used several recommended treatments such as salt (1.23 percent), acetic acid (1:500), formalin (1:4,000), pyridylmercuric acetate or PMA (2 p.p.m.), copper sulfate (0.5 p.p.m.), and potassium permanganate (3 p.p.m.). All of these reagents proved effective in controlling the disease; however, as more experience was gained, we found that potassium permanganate was the most suitable, since it was exhausted after a period of time and the treated tank did not need to be flushed, as was required with the other chemicals.

Chilodon spp.

Only a few outbreaks of disease were attributable to this protozoan, a common ectoparasite of warm-water fishes. Davis (1953) states that this organism may be very destructive to fish crowded in small holding tanks or ponds and has been known to cause serious losses among trout fingerlings.

On a number of occasions, both adult and young tilapia were found to be infested with this parasite. Areas infested were usually the dorsal and caudal fins and along the dorsal surface of the fish, especially near the base of the dorsal fins. Very frequently, trichodinids were also present.

Treatment to rid the fish of this parasite was usually with potassium permanganate or with PMA, although the former was used more extensively because of its ease of application.

Infectious Pancreatic Necrosis

Infectious pancreatic necrosis, until recently known as acute catarrhal enteritis (Lagler, 1956; Snieszko and Wolf, 1958), was the most serious

affliction of young tilapia. Outbreaks of the disease caused high mortality rates among fry about 2 to 3 weeks old, soon after they had started supplementary feeding. Symptoms characteristic of this disease were violent whirling or corkscrewing accompanied by rapid breathing. The afflicted fish usually exhibited a series of these whirling movements, then sank to the bottom of the tank and stopped feeding. Cessation of feeding caused many of the fry to have a "pinhead" appearance, that is, a large head and shrunken body.

These symptoms are similar to those described for octomitiasis, commonly called whirling disease or pinhead condition (Lagler, 1956; Davis, 1953; Snieszko and Wolf, 1958). Octomitiasis is caused by the protozoan *Octomitus salmonis*, which occurs in the intestine either in the flagellated form, when the condition is chronic, or in an intracellular stage, when the disease is acute. The etiology of infectious pancreatic necrosis, on the other hand, is still in doubt, although it has been reported as probably caused by a virus (Lagler, 1956; Snieszko and Wolf, 1958).

All of the symptoms noted here were observed in one particular outbreak of disease at the pilot plant. Dissection and examination of the stomach and anterior intestine of six afflicted fish revealed that only one fish had a protozoan in the intestine. All of the others appeared normal internally. On the assumption that this disease was probably octomitiasis, we started immediate treatment with Carbarsone (p-Ureidobenzene arsonic acid) at the rate of 1 gram per pound of food (Davis, 1953). The mortality rate decreased appreciably in the next few days following treatment and by the end of the tenth day had been reduced to a low level. Although Carbarsone seemingly effected a cure, we are not certain that *Octomitus* was the causative organism, since the protozoan was not positively identified. It might possibly have been infectious pancreatic necrosis, or an acute infection of octomitiasis caused by the intracellular stage of the flagellate, or a combination of the two. Snieszko and Wolf (1958) state that many cases diagnosed as octomitiasis are in reality infectious pancreatic necrosis. Careful microscopic examination is necessary for correct diagnosis.

Subsequent periodic outbreaks of infectious pancreatic necrosis were definitely identified by examination of the stomach and anterior intestine of diseased individuals. In most instances these organs were distended and filled with a colorless, opaque fluid, indicating a stoppage of bile flow. As there is no known effective therapy for this disease, the usual procedure was to treat the fish with potassium permanganate at a concentration of 3 p.p.m. to prevent secondary infection of the weakened fish with ectoparasites and to observe strict sanitation measures. In this way, we believe that most of the disease outbreaks were kept localized.

Mortality rates among the fry were usually highest during the first week after an outbreak and gradually subsided during the following 2 to 3 weeks. The most serious outbreak of disease occurred at the Kewalo plant soon after it was in operation. A succession of infections that spread among the newly emerged fry caused an estimated loss of about 80 percent of the 146,776 fry produced in a 3-month period. The disease was controlled after 10 weeks.

Prophylactic Measures

Despite knowledge that the density of fish is extremely important in relation to the outbreak and spread of disease, we tended to overcrowd our tanks on occasion. Since the amount of fry-rearing facilities was limited, it was impossible to avoid overcrowding during periods of heavy fry production unless we discarded some of the young fish. Our records indicate that several of the disease outbreaks were directly associated with periods of high production. Whenever an overcrowded condition existed, we made every effort to prevent disease outbreaks by increasing the rate of the inflowing water, by cropping the fry-tank compartments frequently, and by observing strict sanitation.

Effective prophylactic measures are probably of greater importance than control measures in successful fish culture. Potassium permanganate was periodically added to the water as a prophylactic measure and, when conditions permitted, tanks which held any diseased fish were thoroughly scrubbed with a brush, refilled with water, and copper sulfate or formalin was added in high concentration. The environment thus created was believed unfavorable to whatever ectoparasites may have remained in the tank after the scrubbing.

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FACTORS AFFECTING FRY PRODUCTION

In commercial bait-rearing operations, it is necessary to obtain maximum production and survival of young from a minimum-sized brood stock. Insofar as possible, optimum conditions of temperature, salinity, food, sex ratio, and brood-stock density are maintained. Some preliminary information was obtained at the pilot plant and more detailed information at the Kewalo plant on the importance of these factors.

TEMPERATURE AND SPAWNING

Fry production started in December 1956 at the pilot plant, and by mid-January 1957 it was apparent that the brood stock in tank 3 was not as productive as that in tank 1.

Environmental conditions in the two tanks differed in several respects. The water temperature in tank 3 averaged 1° to 2° F. cooler than in tank 1. This difference probably arose from the fact that tank 3 was shaded by trees and a storage shed most of the day, whereas tank 1 was situated in more open surroundings and received more hours of direct sunlight. In an attempt to eliminate the temperature difference, the water entering tank 3 was piped through a 100-foot length of black, three-fourths-inch, garden hose that was stretched across the roof of the storage shed. On sunny days, the temperature of the water flowing into tank 3 was raised as much as 5° to 10° F. and the temperature of the water in the tank to about the same level as in tank 1 (table 5).

A second major difference between the tanks was the consistently lower oxygen concentration in tank 3. This condition probably accounted for the dead yolk-sac fry that were frequently found in the detritus siphoned from the floor of the tank. Aeration brought about a significant increase in the concentration of oxygen in tank 3 (appendix table 1).

The pattern of water circulation was also different in the two tanks. The flow of water from inlet to outlet in tank 3 opposed the prevailing wind while that in tank 1 was in the direction of the prevailing wind. The resulting circulation pattern kept tank 1 relatively clean and the water usually green with algae, while tank 3 had much detritus and generally stagnant water. The color of the water in tank 3 varied from clear to light green to dark brown. Improvement in water circulation in tank 3, resulting from aeration and slight heating of the water, was sufficient to produce a significant increase in fry production during March 1957. Tables 6 and 7 give the production per female per month for these brood tanks (tank 2, which was later converted to a brood tank in August 1957, was similar in all respects to tank 1).

TABLE 5.—*Average minimum and maximum temperatures (° F.) in tanks 1 and 3 at the pilot plant*

Month	Tank 1		Tank 3	
	Average temperature		Average temperature	
	Minimum	Maximum	Minimum	Maximum
1957:				
January	70.8	75.6	70.1	75.5
February	69.8	75.2	68.6	75.2
March	71.3	78.0	69.8	78.2
April	71.3	78.0	71.2	78.9
May	72.8	81.3	73.2	81.3
June	74.7	82.3	75.6	82.5
July	74.9	83.3	76.5	82.2
August	75.7	82.6	75.6	81.1
September	(1)	(1)	76.0	81.9
October	(1)	(1)	75.2	80.3
November	72.8	77.0	74.2	78.2
December	70.3	74.5	70.7	74.4
1958:				
January	69.9	74.9	70.2	74.0
February	70.6	76.7	70.7	75.7
March	70.8	77.3	70.8	76.2
April	72.7	79.6	71.6	78.1
May	73.7	80.1	72.8	77.8
June	75.6	82.9	73.8	79.5
July	75.4	82.6	73.9	79.2

[1] No data; thermograph out of order.

TABLE 6.—*Fry produced in tank 1, per female and month, at the pilot plant, December 1956–July 1958*

Month	Brood stock		Number of fry produced		Feed
	Males	Females	Total	Per female [1]	
1956: December	32	64	578	9.0	Chicken mash and rice bran.
1957:					
January	32	64	4,498	70.3	Rice bran.
February	32	64	2,107	32.9	Pondfish feed.
March	32	64	6,433	100.5	Do.
April	32	64	4,050	63.3	Do.
May	32	64	20,297	317.1	Do.
June	31	64	6,146	96.0	Do.
July	31	64	20,910	326.7	Do.
August	31	64	18,520	289.4	Chicken mash.
September	31	64	7,743	121.0	Do.
October	31	64	4,159	65.0	Do.
November	29	64	188	2.9	Alfalfa pellets and pondfish feed.
December	31	64	409	6.4	Do.
1958:					
January	19	59	0	0.0	Pondfish feed.
February	22	61	143	2.3	Do.
March	19	58	48	0.8	Do.
April	19	58	1,418	24.4	Do.
May	17	58	10,701	184.5	Rabbit pellets.
June	17	58	9,158	157.9	Do.
July	12	58	6,172	106.4	Do.

[1] Because of mortalities and transfer of fish, the number of females used to calculate the production per female is based on the number of females that were present in the tank for more than 2 weeks.

TABLE 7.—*Fry produced in tank 3, per female and month, at the pilot plant, December 1956–July 1958*

Month	Brood stock		Number of fry produced		Feed
	Males	Females	Total	Per female [1]	
1956: December	16	32	69	2.2	Chicken mash and rice bran.
1957:					
January	55	93	0	.0	Rice bran and pondfish feed.
February	31	63	374	5.9	Pondfish feed.
March	31	63	1,278	20.3	Do.
April	31	62	8,322	134.2	Do.
May	31	62	13,685	220.7	Do.
June	31	62	9,290	149.8	Do.
July	31	62	14,197	229.0	Do.
August	31	62	9,327	150.4	Do.
September	31	62	2,621	42.3	Do.
October	31	62	1,769	28.5	Do.
November	31	62	1,294	20.9	Do.
December	31	62	274	4.4	Do.
1958:					
January	31	62	32	.5	Do.
February	30	61	147	2.4	Do.
March	29	61	213	3.5	Do.
April	29	61	566	9.3	Do.
May	29	61	3,205	52.5	Rabbit pellets.
June	28	61	78	1.3	Do.
July	20	60	92	1.5	Do.

[1] Because of mortalities and transfer of fish, the number of females used to calculate the production per female is based on the number of females that were present in the tank for more than 2 weeks.

A second experiment in which the effect of temperature on production of young was examined was conducted at the Kewalo plant from January to August 1959.

For tilapia to be most useful as a supplementary skipjack bait, there must be a stock of bait-size fish on hand in May or June, at the beginning of the main fishing season in Hawaiian waters. To achieve this, heavy fry production must be under way by late winter. Brock and Takata (1955: p. 24) reported that tilapia spawn throughout the year in Hawaiian waters, but that the spawning is less intense during the winter months. Consequently, an experiment was conducted at the Kewalo plant to determine if raising water temperatures would induce tilapia to spawn at a high rate during the winter months. Three redwood tanks (tanks 13, 14, and 15) were arranged as follows for the experiment:

1. Tank 13 was not modified in any way and served as the control.

2. The water in tank 14 was artificially heated with a 60-foot, lead-sheathed heating cable rated 3.63A–115V, that produced 400 watts, or 6.7 watts per foot. A thermostat with a capillary tube was placed in the tank to control the temperature. A cover made of sisal-glaze, a clear, longlasting plastic, was placed over the tank (fig. 8) to prevent excessive heat loss, especially at night.

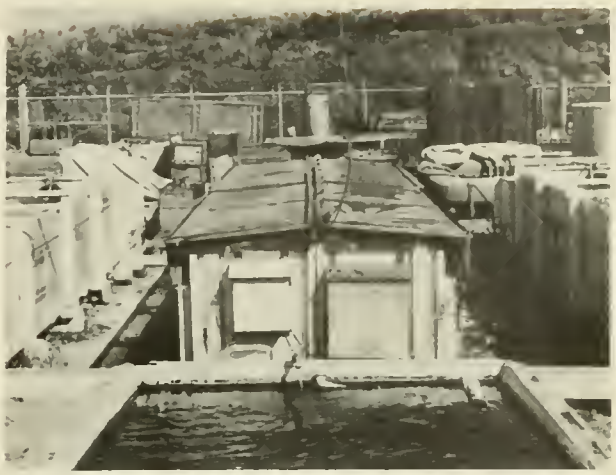

FIGURE 8.—Plastic cover over artificially heated tank 14.

3. The water in tank 15 was also artificially heated with the same type of heating cable used in tank 14, but the tank was not covered to prevent heat loss.

Each tank was stocked with 32 males and 64 females and fed trout feed. Emerging fry were collected and counted daily. The daily variation in water temperature was recorded by thermographs and minimum and maximum thermometers.

The production per female per month and the average and range of minimum and maximum temperatures for each of the three tanks are recorded in table 8 and shown graphically in figure 9. In January, tank 14, which was modified with heating cable and cover, had relatively better production than the other two tanks. In February, artificial heating was started in tank 15, and resulted in a marked increase in production comparable to that in tank 14. Production was still low in the control tank. In March, with rising air temperatures the water warmed in all three tanks and production increased in all; however, the increase in the slightly warmed tank 15 greatly exceeded that in the other tanks. Temperatures remained about the same in April, but production dropped, particularly in tanks 14 and 15. With higher temperatures in May, the control tank maintained its slight lead over tank 15, and during the last 3 months of the experiment, it outproduced the two artificially heated tanks by a significant margin. Over the course of the experiment, total fry production in tank 13 (control) was about twice that in the other two tanks.

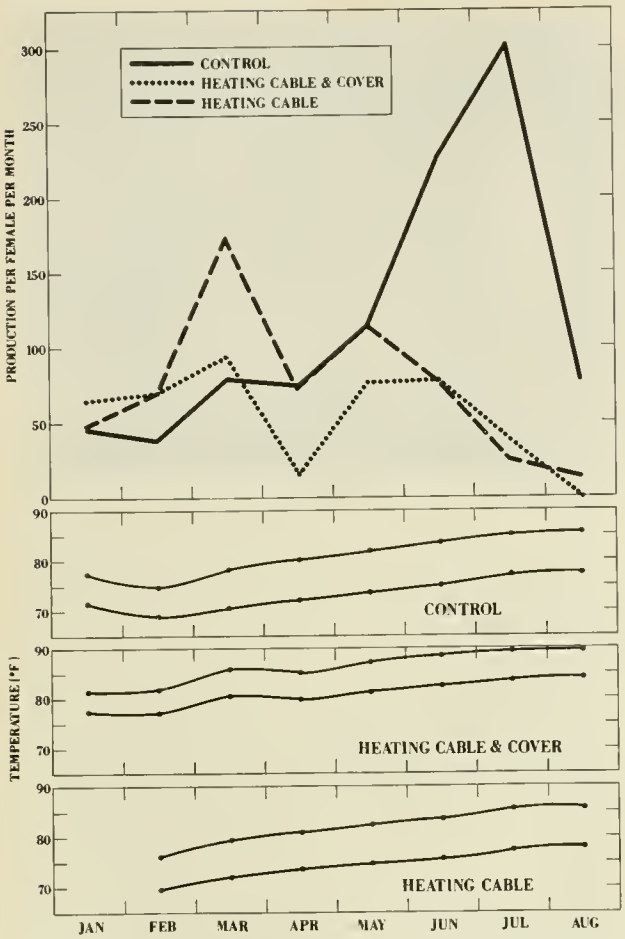

FIGURE 9.—Production per female per month in the heated tanks and in the control tank, and average minimum and maximum water temperatures in the tanks.

Analysis of the data indicates that although some increase in spawning was induced during the winter months by raising the water temperature, the increase in production was not great. In addition, only a slight rise in water temperature apparently produced the same results as a marked increase in temperature. The results also indicate that prolonged or constant high temperatures may be detrimental to spawning. Innes (1951) pointed out that at constant high temperatures the oxygen content of the water becomes diminished and this seems to have a weakening effect on fish. Doudoroff (1957: p. 415) stated—

> that persistent nonlethal deficiency of dissolved oxygen undoubtedly can adversely influence the activities of fishes and have serious detrimental effects on fish populations in their natural environments.

The oxygen record (appendix table 4) discloses that throughout the period of the experiment, tank 14 had generally lower concentrations of oxygen, which may account for the decrease in fry production during the summer months.

Although tanks 13 and 15 had similar temperatures, fry production in these two tanks differed significantly for the months of June to August. While it is true that tank 15 was heated artificially (thermostat set at 80° F.), much of the heat was lost through convection. Thus, tank 15 remained only slightly warmer than the control tank. The average temperatures in both tanks fell within the optimum temperature range for propagation, which is from 20° to 35° C. (68° to 95° F.) according to Chen (1953), while the weekly oxygen determinations showed very little difference between the two tanks. We are unable to advance a satisfactory explanation for the poor fry production in tank 15.

TABLE 8.—*Summary: Fry production and temperatures of brood tanks used in the heating experiment, January–August, 1959*

[Temperature ° F.]

Month	Number of fry produced		Average temperature		Temperature range	
	Total	Per female	Minimum	Maximum	Minimum	Maximum
Tank 13 (control):						
January	2,967	46.4	71.4	77.4	63.0	83.4
February	2,492	38.9	67.9	74.8	64.2	78.5
March	5,032	78.6	70.6	78.2	67.7	81.9
April	4,739	74.0	72.1	80.1	67.1	84.6
May	7,365	115.1	73.5	81.8	70.1	86.4
June	14,456	225.9	75.0	83.6	72.6	86.2
July	19,319	301.8	77.0	85.1	74.3	90.4
August	5,010	78.3	77.3	85.4	72.3	90.3
Total	61,380					
Tank 14 (with heating cable and cover):						
January	4,064	63.5	77.3	81.4	72.1	88.3
February	4,448	69.5	77.2	81.8	74.8	84.6
March	5,922	92.5	80.4	85.9	78.0	88.0
April	992	15.5	79.8	85.2	76.0	90.7
May	4,804	75.1	81.2	87.2	76.8	90.2
June	4,935	77.1	82.5	88.6	81.0	90.6
July	2,376	37.1	83.5	89.4	79.0	90.9
August	0	0.0	84.1	89.5	79.8	90.9
Total	27,541					
Tank 15 (with heating cable):						
January	3,046	47.6				
February	4,424	69.1	69.6	76.0	65.0	78.0
March	11,166	174.5	72.1	79.6	69.0	83.0
April	4,660	72.8	73.6	81.0	69.0	85.0
May	7,269	113.6	74.8	82.6	72.0	87.0
June	4,905	76.6	75.7	83.7	73.6	85.4
July	1,555	24.3	77.3	85.4	74.0	89.9
August	822	12.8	77.9	85.6	72.8	89.4
Total	37,847					

SEX RATIO AND BROOD-STOCK DENSITY

A ratio of 2 ♀ : 1 ♂ was used initially at the pilot plant and judged to yield satisfactory results. The best production resulting from this sex ratio was realized during July 1957 at the pilot plant, when production in tank 1 amounted to 20,910 fry or 327 fry per female (table 6). A second grouping of 5 ♀ : 1 ♂ (total stock, 72) was also tried in tank 2 from August to November, 1957. The production per female per month is given in table 9. The best production for that period and grouping occurred in August, when fry production amounted to 2,532, or 42 fry per female.

TABLE 9.—*Production of fry per female per month in tank 2 at the pilot plant, August 1957–July 1958*

Month	Brood stock		Number of fry produced		Feed
	Males	Females	Total	Per female[1]	
1957:					
August	12	60	2,532	42.2	Pond-fish feed.
September	12	60	2,383	39.7	Do.
October	12	60	1,535	25.6	Do.
November	12	60	0	0.0	Do.
December	16	56	107	1.9	Do.
1958:					
January	16	56	3	0.1	Do
February	16	56	2,891	51.6	Do.
March	16	56	7,691	137.3	Do.
April	16	56	6,660	118.9	Do.
May	31	72	11,627	161.5	Rabbit pellets.
June	31	72	19,826	275.4	Do.
July	29	72	7,781	108.1	Do.

[1] Because of mortalities and transfer of fish, the number of females used to calculate the production per female is based on the number of females that were present in the tank for more than 2 weeks.

A more detailed experiment designed to determine the ideal sex ratio for maximal yield of fry was conducted at the Kewalo plant from September to November 1958. The effect of brood-stock density on spawning was simultaneously investigated in the same experiment.

The 12 assault boats mentioned earlier were stocked with various sex ratios and concentrations of fish. The design of this partially confounded factorial experiment is shown in table 10. The brood stock was fed dry trout feed at the rate of 2 percent of its weight daily. It was assumed that any differences in temperature or oxygen concentrations which might occur among the tanks would not bias the results.

TABLE 10.—*Sex ratios and concentrations of tilapia used to stock the 12 assault-boat tanks, September–November 1958*

Sex ratio (♀:♂)	Sex ratio in concentration of							
	30 fish		50 fish		70 fish		90 fish	
	♀	♂	♀	♂	♀	♂	♀	♂
2:1	20	10	33	17	47	23		
3:1	23	7	38	12			68	22
4:1	24	6			56	14	72	18
6:1			43	7	60	10	77	13

The experiment was terminated after 13 weeks. An analysis of variance of the data (table 11) indicated significant differences ($F=5.73$, $P < 0.01$) between fry production with respect to the sex ratios used in the experiment. (A probability level of 5 percent is considered the maximum value for a conclusion of significance in this report.) The most productive ratio was 3 ♀ : 1 ♂ (tanks 4 and 5). Tanks 1 and 2 with a ratio of 2 ♀ : 1 ♂ were almost equally high in production for the first 2 months of the experiment (fig. 10).

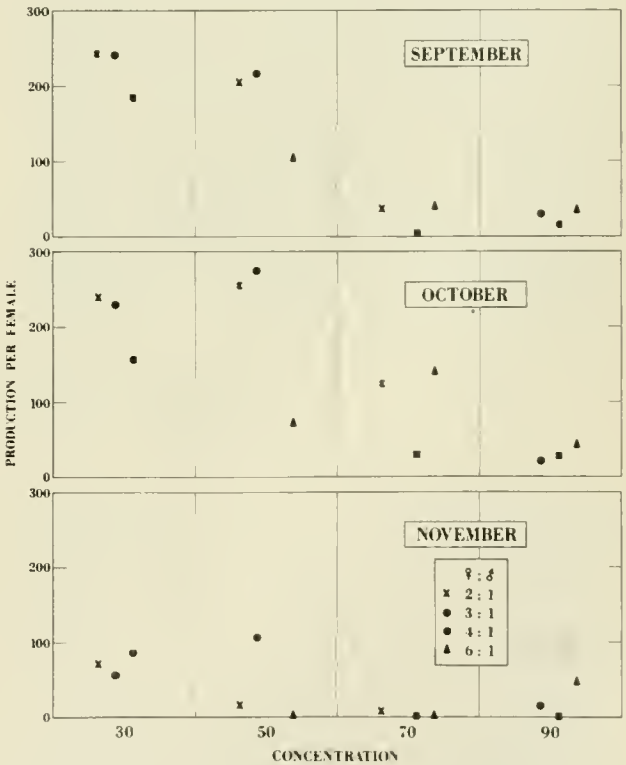

FIGURE 10.—Production per female in relation to sex ratios and concentrations of brood stock.

The relation between total production per female and bottom area (square feet) per male is shown in figure 11, while the total production per female in relation to bottom area per individual is shown in figure 12. From table 11 and

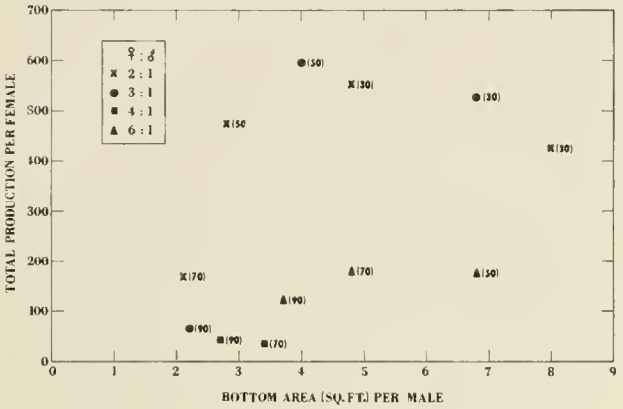

FIGURE 11.—Total production per female in relation to bottom area (sq. ft.) per male. (Total stock in parentheses.)

figures 10 to 12, it may be seen that the tanks with 50 fish or less (except tank 10) had a much better production than those with more, while an allowance of 4 square feet of bottom area per male and 1 square foot per individual gave the highest production per female (see tank 5, table 11).

The analysis of variance showed that the differences in fry production with respect to the concentrations, 30, 50, 70, and 90 fish, used in the experiment were significant ($F = 11.44$, $P < 0.01$). There was also a significant interaction between sex ratios and brood-stock density, indicating that the production resulting from any specific ratio did not vary in a uniform manner with respect to availability of space.

DIET AND REPRODUCTION

Early attempts to assess the qualities of different types of feed in relation to fry production at the pilot plant proved inconclusive, owing to dissimilar conditions in the brood tanks (tanks 1 and 3). However, we were able to observe the general acceptability of the five types of feed that were used.

Finely ground feed, such as rice bran and chicken mash, was found to be unsuitable for the adults as they cannot strain small particles from the water. Much of the feed was wasted and

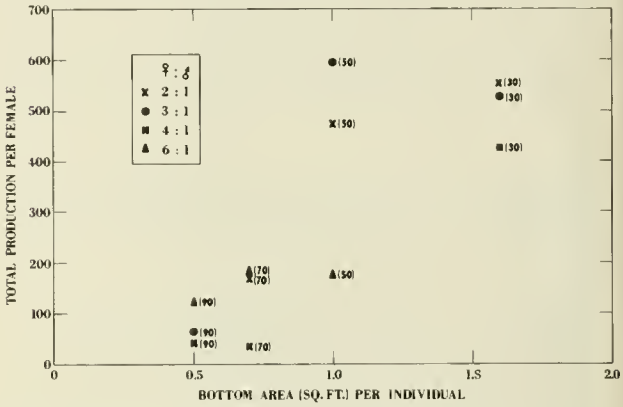

FIGURE 12.—Total production per female in relation to bottom area (sq. ft.) per individual. (Total stock in parentheses.)

TABLE 11.—*Sex ratio and concentration of brood stock and production of fry, September–November, 1958*

Item	Tank No. —											
	1	2	3	4	5	6	7	8	9	10	11	12
Sex ratio (♀:♂)	2:1	2:1	2:1	3:1	3:1	3:1	4:1	4:1	4:1	6:1	6:1	6:1
Number of fish:												
Females	20	33	47	23	38	68	24	56	72	43	60	77
Males	10	17	23	7	12	22	6	14	18	7	10	13
Total fish	30	50	70	30	50	90	30	70	90	50	70	90
Bottom area (sq. ft.):												
Per male	4.8	2.8	2.1	6.8	4.0	2.2	8.0	3.4	2.7	6.8	4.8	3.7
Per fish	1.6	1.0	0.7	1.6	1.0	0.5	1.6	0.7	0.5	1.0	0.7	0.5
Production:												
September:												
Fry produced	4,872	6,762	1,723	5,567	8,209	2,077	4,426	272	1,043	4,459	2,471	2,627
Fry per female	243.6	204.9	36.6	242.0	216.0	30.5	184.4	4.8	14.5	103.7	41.2	34.1
October:												
Fry produced	4,775	8,402	5,891	5,292	10,443	1,396	3,766	1,620	1,955	3,099	8,376	3,089
Fry per female	238.8	254.6	125.3	230.1	274.8	20.5	156.9	28.9	27.2	72.1	139.6	40.1
November:												
Fry produced	1,441	504	334	1,287	4,036	921	2,054	20	37	28	36	3,564
Fry per female	72.0	15.3	7.1	56.0	106.2	13.5	85.6	0.4	0.5	0.6	0.6	46.3
Total:												
Fry produced	11,088	15,668	7,948	12,146	22,688	4,394	10,246	1,912	3,035	7,586	10,883	9,280
Fry per female	554.4	474.8	169.1	528.1	597.0	64.6	426.9	34.1	42.2	176.4	181.4	120.5

tended to foul the tanks. On the other hand, pelletized feed, such as pondfish and trout feed, was consumed by the adult fish with little wastage. Rabbit feed had a high percentage of crude fiber, which seemed to pass through the fish undigested and left much residue in the tank. Alfalfa pellets were somewhat less acceptable than the other feeds mentioned, probably because of their large size and their high fiber content.

An experiment to evaluate the effects of different types of feed in relation to fry production was conducted at the Kewalo plant in September-November, 1958. For this experiment, the three redwood tanks (tanks 13, 14, and 15) were each stocked with 32 males and 64 females. The adults in tank 13 were fed trout feed, which we believed to be high in nutritional value and which was relatively expensive. Those in tank 14 were fed rabbit feed. As stated earlier, this feed was acceptable to the tilapia and was also much cheaper than trout feed. Preliminary trials at the pilot plant indicated that relatively good fry production was possible with this feed. The fish in tank 15 were fed millrun, which was locally produced and the least expensive of the feeds tested.

Table 12 gives the production per female for the 3 months that the experiment was conducted. A plot of the number of fry per female per month is shown in figure 13. It is evident that the fish that were fed trout feed (tank 13) produced the greatest number of fry per female, while the fish that were fed rabbit feed (tank 14) and millrun (tank 15) had very low fry production.

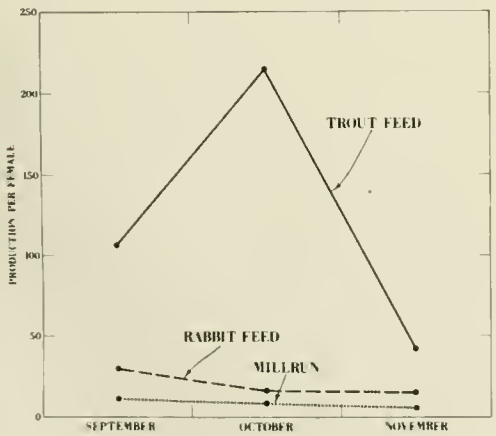

FIGURE 13.—Effect of type of feed given brood stock on production per female.

TABLE 12.—*Production per female in three brood tanks, by type of feed, September–November, 1958*

[Each tank stocked with 32 males and 64 females]

	Tank 13 (trout feed)	Tank 14 (rabbit feed)	Tank 15 (millrun)
September:			
Fry produced	6,863	1,874	751
Fry per female	107.2	29.3	11.7
October:			
Fry produced	13,769	1,074	529
Fry per female	215.1	16.8	8.3
November:			
Fry produced	2,695	982	394
Fry per female	42.1	15.3	6.2
Total:			
Fry produced	23,327	3,930	1,674
Fry per female	364.5	61.4	26.2

Temperature was not considered a factor in fry production in this experiment, since there was very little difference in water temperatures among the tanks. Assuming that other environmental factors were similar among the tanks, it follows from this experiment that the use of a nutritionally balanced feed is highly important in obtaining good fry production. We are not certain, however, of the long-range effect of such high-protein feeds on tilapia, which are principally herbivorous. These trout feeds are manufactured primarily for trout culturists who intend to market the fish rather than use them as brood stock—they may possibly be detrimental to spawning fish. Schaeperclaus (1933: p. 98) stated that the ovaries of trout—under intensive artificial feeding—degenerate and produce few usable eggs. It is likely that spawning stocks of tilapia held for extended periods of time should be fed a diet more in keeping with their natural food or be replaced after a year or two by a new stock of brood fish grown under more natural conditions.

SALINITY AND SPAWNING

During the summer of 1959, the Hawaii Division of Fish and Game started plans for construction of a tilapia hatchery in an area with free accesss to brackish water (about 10 °/₀₀). At the Division's request, experiments dealing with spawning and growth of young tilapia in brackish water were initiated at the Kewalo plant.

Several investigators have observed and reported that tilapia will spawn in a saline environment. Vaas and Hofstede (1952: p. 11, 16) reported that spawning occurred in a period during which the salinity of the water ranged from 3 to 4.8 percent. They pointed out, however, that "Ac-

cording to subsequent findings of the Extension Service in Indonesia, good growth is limited by a salinity of 4 percent and spawning by one of 3 percent." Brock (1954) reported tilapia spawning in sea water of a chlorinity of 19.29 °/₀₀ (equal to a salinity of about 34.85 °/₀₀) and a pH of 7.95.

Four tanks were used in this experiment: two test tanks contained brackish water and two controls contained fresh water. The experiment was started in August 1959 and terminated during the latter part of September when heavy mortalities among the adults caused by either asphyxiation or hydrogen sulfide occurred in both brackish-water tanks. Each tank was stocked with 36 females and 12 males, that is, with a 3:1 sex ratio, and at a concentration of 1 square foot per individual.

The yield of fry for the 2 months of the experiment is given in table 13. The total production was almost three times as great from the treatment tanks (brackish water) as from the controls. Analysis of variance indicated a significant difference ($F=472.65$, $P<0.05$) between fry production with respect to brackish- and fresh-water methods of culture, but no significant difference between replicates.

Exactly what influence the saline environment exerts in bringing about this increased fry production is not known, but the results of this experiment emphasize the desirability and possibilities of tilapia culture in brackish water.

TABLE 13.—*Fry production in brackish-water and fresh-water tanks, 1959*

	August	September	Total
BRACKISH WATER			
Salinity (°/₀₀):			
Minimum	8.9	9.4	
Maximum	12.3	15.2	
Average	10.9	13.2	
Tank 1:			
Fry produced	11,845	15,519	27,364
Fry per female	329.0	431.1	
Tank 3:			
Fry produced	17,319	11,745	29,064
Fry per female	481.1	326.2	
FRESH WATER			
Tank 5:			
Fry produced	6,479	1,169	7,648
Fry per female	180.0	32.5	
Tank 12:			
Fry produced	8,910	2,172	11,082
Fry per female	247.5	60.3	

FACTORS AFFECTING GROWTH OF YOUNG

The effects of environmental factors on growth of young tilapia were studied experimentally at the Kewalo plant for 12 weeks, beginning in April 1959. The effects of space or density of the fish, diet, and salinity were examined during the experiment.

We tried to vary one factor at a time, keeping the others constant, so that the single factor under observation could be evaluated with some degree of precision. We did not attempt to control the temperature, since differences among the tanks were not significant. Other factors, such as volume of water in the tank and the rate of water flow, were held as uniform as possible. In each experiment, the fish were fed at the same rate per fish regardless of lot size. An excellent quality trout feed was fed to the fish twice a day, except weekends, at the regular feeding times.

Once each week, length and weight measurements were made on a randomly collected subsample from each tank under observation. All of the fish in the subsample were returned to their respective tanks after measurements were completed. The number of fish in a subsample varied with each experiment.

We realize that, ideally, all phases of the experiments should have been conducted simultaneously. This was not possible, however, because of a lack of sufficient quantities of fry. As a result, different phases of the experiments were commenced as fry became available in adequate amounts to stock the tanks.

CONCENTRATION OF FISH AND GROWTH

A series of tests to determine the rate of growth of young tilapia in relation to their concentration, or the amount of space available for growth, was started at the Kewalo plant in April 1959. Five lots of fry, ranging in number from 1,000 to 6,000, were placed in the assault-boat tanks; however, all tanks were not stocked simultaneously.

The fish were fed trout feed (starter, fry, and small fingerling grades) for 12 weeks. The particle size and amount of feed was gradually increased as growth progressed. The fish were fed twice daily except on weekends, when they were fed once a day.

Twenty-five fish were measured from each of the lots of 1,000, 2,000, and 3,000 fish, 40 from the lot of 4,000 fish, and 50 from the lot of 6,000 fish. Table 14 gives the weekly averages of length and weight of fish in the randomly collected subsamples, while figure 14 shows the regression lines fitted to the growth data.

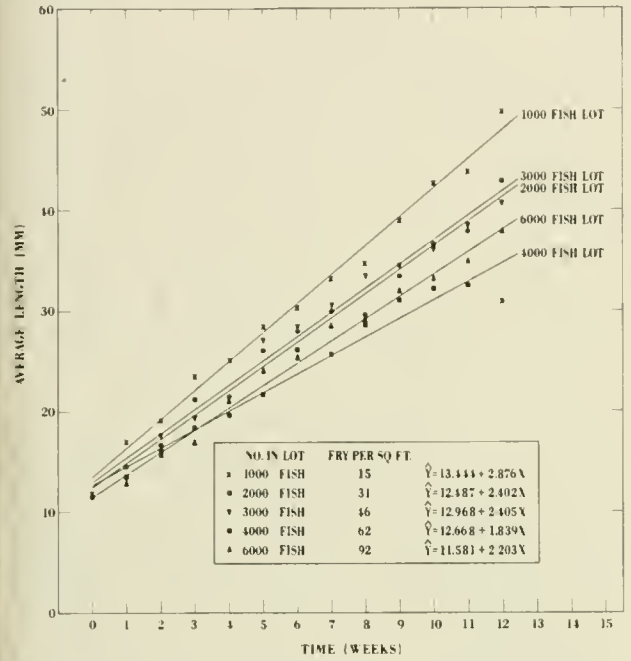

FIGURE 14.—Regression of length on time for five lots of tilapia reared in various concentrations of fish in tanks.

Examination of the regression coefficient from each lot indicated that young in the tank stocked with 1,000 fish had the best growth rate (2.9 mm. per week) during the 12-week period, and that growth rates were somewhat slower with an increasing number of fish per lot. Fish in tanks stocked with 2,000 and 3,000 fry had almost identical growth rates (2.4 mm. per week) but less favorable growth than the 1,000-fish lot. The lot of 6,000 fish, for some unknown reason, had a better growth rate than the lot containing 4,000 fish (2.2 and 1.8 mm., respectively, per week).

Statistically, the differences in growth among the five lots of fish were significant ($F=41.92$, $P<0.01$). From the results of the experiment, it follows that the ideal stocking density for nursery waters (fry tanks) would be 9 fry per cubic foot or 15 fry per square foot of surface area (1,000-fish lot). Some lesser concentration, as yet undetermined, might prove even better. However, from a practical standpoint, these very low stocking rates might not be the most feasible economically, as the space requirements and construction costs for fry-rearing tanks would be enormous in a commercial operation.

TABLE 14.—*Weekly average length (mm.) and weight (g.) and average absolute growth rates in random subsamples of tilapia from various concentrations of fry, 1959*

	1,000 fry	2,000 fry	3,000 fry	4,000 fry	6,000 fry
Experiment began	May 29	May 29	Apr. 9	May 22	Apr. 9
Experiment ended	Aug. 21	Aug. 21	July 2	Aug. 14	July 2
Initial length	12.4	12.0	11.9	11.8	11.9
Initial weight	0.024	0.012	0.024	0.012	0.024
1st week:					
Length	17.0	14.5	13.6	13.5	12.8
Weight	0.072	0.040	0.040	0.030	0.040
2d week:					
Length	19.2	16.7	17.6	16.0	15.7
Weight	0.116	0.068	0.096	0.052	0.062
3d week:					
Length	23.5	21.2	19.3	18.3	16.8
Weight	0.168	0.148	0.094	0.092	0.062
4th week:					
Length	25.1	21.5	25.0	19.7	21.1
Weight	0.284	0.176	0.272	0.115	0.148
5th week:					
Length	28.3	26.1	27.2	21.7	24.0
Weight	0.400	0.320	0.308	0.152	0.224
6th week:					
Length	30.3	28.0	28.4	26.2	25.3
Weight	0.480	0.400	0.416	0.312	0.264
7th week:					
Length	33.2	29.9	30.6	25.7	28.4
Weight	0.640	0.492	0.500	0.300	0.432
8th week:					
Length	34.7	29.6	33.5	28.6	29.2
Weight	0.792	0.500	0.705	0.412	0.484
9th week:					
Length	39.1	33.4	34.5	31.1	31.9
Weight	1.116	0.692	0.780	0.578	0.628
10th week:					
Length	42.7	36.6	36.2	32.2	33.2
Weight	1.448	0.960	0.844	0.605	0.670
11th week:					
Length	43.8	37.8	38.4	32.5	34.8
Weight	1.596	0.964	0.964	0.615	0.708
12th week:					
Length	49.8	42.8	40.7	30.8	37.8
Weight	2.408	1.528	1.280	0.612	0.972
Average absolute growth rate	3.1 mm.	2.6 mm.	2.4 mm.	1.6 mm.	2.2 mm.

Earlier, we mentioned that newly emerged fry almost always were captured near the surface of the water. Upon transfer to nursery waters, the fry continue to exhibit this behavior. Therefore, we believe that stocking density should be related to surface area rather than to volume of water.

DIET AND GROWTH

An experiment to compare the growth rates obtained on an inexpensive, commercially available feed and the more expensive, but highly nutritious, trout feed was initiated in April 1959 simultaneously with the experiment on relation of space to growth at the Kewalo plant. An as-

sault-boat tank was stocked with 3,000 fry and fed exclusively with wheat white middlings, a locally available livestock feed, while the lot of 3,000 fry in the space-growth experiment was fed trout feed.

The weekly average lengths and weights of a random subsample of 25 fish from each of the two lots, for the 12-week period of the experiment, are presented in table 15. Regression lines were fitted

TABLE 15.—*Weekly average length (mm.) and weight (g.) and average absolute growth rates in random subsamples of tilapia from 2 lots of 3,000 fry reared on different diets, 1959*

Item	Trout feed	Wheat white middlings
Experiment began	Apr. 9	May 15
Experiment ended	July 2	Aug. 7
Initial length	11.9	12.1
Initial weight	0.024	0.014
1st week:		
Length	13.6	13.7
Weight	0.040	0.032
2d week:		
Length	17.6	16.9
Weight	0.096	0.064
3d week:		
Length	19.3	18.9
Weight	0.094	0.104
4th week:		
Length	25.0	21.0
Weight	0.272	0.160
5th week:		
Length	27.2	21.5
Weight	0.308	0.144
6th week:		
Length	28.4	23.5
Weight	0.416	0.424
7th week:		
Length	30.6	27.1
Weight	0.500	0.392
8th week:		
Length	33.5	28.6
Weight	0.705	0.380
9th week:		
Length	34.5	30.3
Weight	0.780	0.520
10th week:		
Length	36.2	31.7
Weight	0.844	0.620
11th week:		
Length	38.4	34.0
Weight	0.964	0.672
12th week:		
Length	40.7	33.9
Weight	1.280	0.768
Average absolute growth rate	2.4 mm.	1.8 mm.

to the growth obtained in these tanks. The regression coefficient for the lot fed trout feed was 2.4 mm. per week while that for the lot fed wheat white middlings was 1.9 mm. per week (fig. 15). An analysis of variance of the results disclosed a significant difference in growth rates between the fish in the two tanks ($F=31.09$, $P<0.01$), indicating that quality of the feed is highly important where fast growth rates are desired.

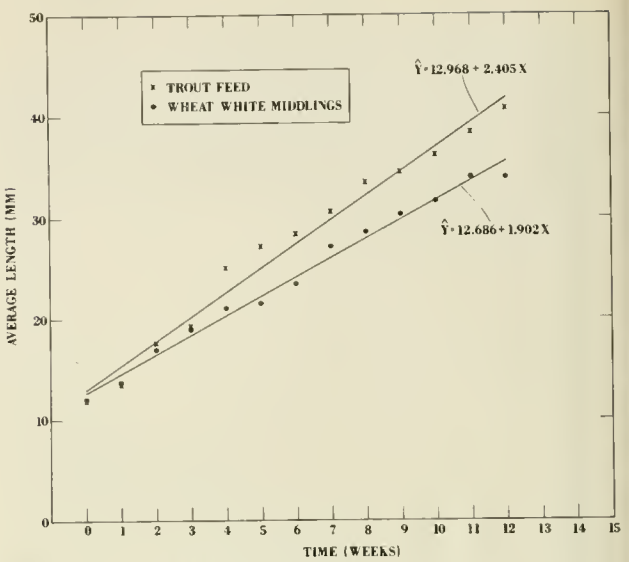

FIGURE 15.—Regression of length on time for two lots of fish reared on different diets.

SALINITY AND GROWTH

It has been reported by Vaas and Hofstede (1952) and Brock (1954) that *T. mossambica* will spawn and the young will grow in salt water. To determine growth rates under varying degrees of salinity, preliminary experiments were conducted at the Kewalo plant laboratory using 30-gallon aquariums.

Five 30-gallon aquariums were used in the experiment: two containing fresh water, two brackish water (salinity of about 16 °/₀₀, and one sea water. Each aquarium was stocked with 200 fry. Those fish to be tested in brackish water and in sea water were acclimatized to sea water for a period of 24 hours before being placed in the aquariums. The fish in one tank in each pair of the fresh-water and brackish-water aquariums were fed wheat white middlings, while fish in the other two tanks and in the sea-water tank were fed trout feed (starter).

From the first week, a large number of deaths occurred in the brackish- and sea-water tanks and the deaths continued to occur for several weeks. At first, the dead fish in each of the tanks were removed and counted each morning and replaced with an equal number of individuals of similar size from a reserve stock which was held in sea water in another aquarium. Because of the high mortality rate and the low growth rate in all the

TABLE 16.—*Differences in average length (mm.), weight (g.) and average absolute growth rates of 5 lots of 200 fish, in relation to types of water and feed*

Item	Aquarium No.—				
	1	2	3	4	5
Type of water	Fresh	Fresh	Brackish	Brackish	Sea.
Type of feed	Trout	Wheat white middlings.	Trout	Wheat white middlings.	Trout.
Initial length of fry	12.8	13.3	13.3	13.2	13.0.
Initial weight of fry	0.03	0.03	0.03	0.03	0.03.
Length at 5 weeks	17.9	18.3	17.8 [1]	18.0	18.2.
Weight at 5 weeks	0.12	0.12	0.10	0.12	0.14.
Average absolute growth rate	1.02 mm.	1.00 mm.	0.90 mm.	0.96 mm.	1.04 mm.
Total deaths	66	95	122	208	333.

[1] These figures are based on length-weight measurements at end of the fourth week.

experimental tanks, the experiment was terminated at the end of 5 weeks.

A random subsample of 10 fish was collected from each aquarium and the fish measured once each week during the 5-week period (table 16). The results were not suitable for statistical analysis. A general summary (table 16) shows that mortality was lowest in fresh water and highest in sea water. Differences in growth rate were slight and most likely of no biological significance.

A second experiment, which dealt with the effects of salinity on growth of the young, was conducted simultaneously with the experiment on

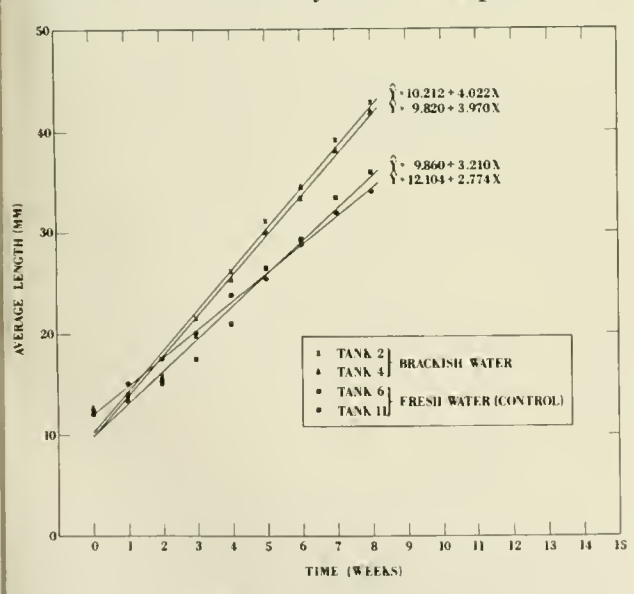

FIGURE 16.—Regression of length on time for young tilapia reared in brackish and in fresh water.

the effect of salinity on the rate of reproduction.

Four assault-boat tanks, two containing brackish water with a salinity of about 10 °/₀₀ and two with fresh water serving as controls, were stocked simultaneously with 4,000 fry. The fish were fed trout feed twice a day. Salinity determinations (by hydrometer) of the brackish-water tanks were made daily (table 13 lists average and range of salinities for the 2 months of the experiment). Length and weight measurements were made weekly for 8 weeks on a random subsample of 40 fish from each tank. The results of the experiment are recorded in table 17, while the regression lines describing the growth in each tank are shown in figure 16.

It is evident from the regression coefficients that the brackish-water environment had a pronounced influence on the growth rate of the young fish. Here again, we are not certain of the effect of the saline environment on young tilapia, but presumably it alters metabolic processes enough to affect growth considerably. An analysis of variance indicated a significant difference in growth between treatments ($F=39.94$, $P<0.01$), and no significant difference in growth between replicates.

Another interesting aspect of this experiment was that the growth rates of the fish in the fresh-

TABLE 17.—*Average length (mm.) and weight (g.) and average absolute growth rates of random subsamples of tilapia from 4 lots of 4,000 fry reared in brackish and fresh water*

Item	Brackish water		Fresh water	
	Tank 2	Tank 4	Tank 6	Tank 11
Initial length	12.4	12.6	12.0	12.1
Initial weight	0.028	0.030	0.025	0.025
1st week:				
Length	14.1	13.5	15.2	13.5
Weight	0.042	0.040	0.055	0.042
2d week:				
Length	15.8	15.5	17.6	15.2
Weight	0.070	0.072	0.080	0.065
3d week:				
Length	21.6	19.8	20.2	17.5
Weight	0.178	0.145	0.265	0.225
4th week:				
Length	26.2	25.3	23.8	21.0
Weight	0.295	0.280	0.242	0.145
5th week:				
Length	31.2	29.9	25.4	26.5
Weight	0.548	0.500	0.300	0.380
6th week:				
Length	33.4	34.5	28.8	29.3
Weight	0.772	0.892	0.490	0.512
7th week:				
Length	39.2	38.1	32.0	33.4
Weight	1.200	1.100	0.632	0.712
8th week:				
Length	42.8	41.8	34.1	36.0
Weight	1.412	1.378	0.682	0.870
Average absolute growth rate	3.8 mm.	3.6 mm.	2.8 mm.	3.0 mm.

water control tanks compared favorably with the growth rates of the 1,000-fish lot in the space-growth experiment. We expected that the growth rates in the control tanks would be somewhat similar to those experienced in the 4,000-fish lot of the space-growth experiment. The growth rates in the two control tanks were 3.2 and 2.8 mm. per week over an 8-week period, while the growth rate of the 4,000-fish lot was 2.1 mm.

The fish were raised under seemingly identical conditions, except for the time of year that the experiment was conducted. The 4,000-fish lot was reared from mid-May to mid-August, while the control-tank lots were reared in August and September. Although there are no temperature records for these growth experiments, the temperature record of the heating experiment (table 8) discloses a difference of about 4° F between May and August in control tank 13. Presumably, this difference also applied to the assault-boat tanks. Therefore, it is quite reasonable to conclude that water temperature is important in obtaining fast growth; however, the optimum temperature has not been determined.

Some other factor, possibly environmental, chemical, or genetic, acting singly or in combination with temperature may also have contributed to this discrepancy in growth rates. The end results of the salinity-growth experiment paralleled the results of the salinity-spawning experiment, however, indicating that a commercial rearing plant can, and should be operated on a brackish-water system, thereby reducing or eliminating the high cost of using fresh water.

CANNIBALISM AND PREDATION

Cannibalism and predation are important factors in the successful rearing of young tilapia. Our initial plan to rear tilapia fry to bait-fish size in a single large fry tank met with a major setback when about 2 months after production started we discovered juveniles, ranging in length from 25 to 38 mm. (1 to 1.5 in.), chasing and consuming newly emerged fry that were being released into the tank. This situation was remedied by installing Monel-screen partitions to separate the tank into three compartments and segregate the young according to size. Cannibalism among tilapia was also reported by Chen (1953). The results of his observations are summarized in table 18.

TABLE 18.—*Size relation between intraspecific predator and prey in* T. mossambica

[Data from Chen (1953)]

Size of predator	Size of prey
0.75 inch	Up to 0.38 inch.
3 to 6 inches	Up to 0.5 inch.
7 inches	Up to 1.25 inches.

In order to extend the findings of Chen and further define this intraspecific, predator-prey size relation, the following experiments were conducted in 35-gallon aquariums. Eight juvenile groups (predator) of different average lengths were selected. The average length of the groups ranged from 20.4 to 64.4 mm. (about 0.75 to 2.5 in.). A predator group consisting of 10 juveniles was first measured and placed in an aquarium. A second group of 20 to 30 young (prey), all fry or fry and juveniles, was also measured and placed in the same aquarium. Each of the eight experiments was carried out for a period of 72 hours, after which time the remaining prey were removed and measured. The fish did not receive any supplementary feeding during the period of the experiment. By comparing the lengths of the remaining young with the lengths of the young that were put into the aquarium, we were able to determine the maximum size of the young that were killed or consumed by each size group of predators. The results are given in table 19 and figure 17.

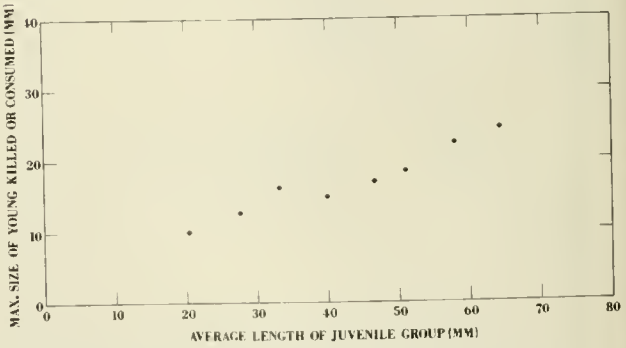

FIGURE 17.—Relation between size of juvenile groups (predators) and maximum size of young killed or consumed.

TABLE 19.—*Size of young (prey) killed and consumed by different juvenile groups (predator)*

[A juvenile group consisted of 10 fish of approximately equal size]

Length of predator group (mm.)		Length of prey group (mm.)	
Range	Average	Range	Maximum size killed
18.3–23.7	20.4	9.7–12.5	10.0
24.2–29.6	27.6	10.2–15.6	12.7
30.4–36.4	33.2	9.8–19.2	16.2
36.9–42.3	40.0	10.3–19.2	15.0
43.2–48.7	46.7	9.8–20.0	17.0
49.4–54.8	51.0	9.0–21.2	18.5
55.7–61.4	58.0	9.0–29.0	22.5
62.0–67.8	64.4	9.2–29.0	24.5

Other experiments with starved and well-fed juveniles showed that the degree of cannibalism increases when the fish are starved. One particular group of 50 juveniles, averaging 31.8 mm. (1.25 in.) in length, when well fed consumed 9 fry averaging 11.1 mm. (0.44 in.) in 15 minutes. This same group, when starved for a period of 3 days, killed or consumed 17 fry averaging 14.3 mm. (0.56 in.) in 12 minutes. When starved, the juveniles were aggressive upon introduction of the fry, whereas when well fed they were not particularly excited by appearance of the fry and generally remained near the bottom of the tank. An aggressive response by well-fed juveniles was noticeable only when a single fry or group of fry approached closely.

These experiments indicated the importance of keeping each compartment of the fry tank stocked with young fish of uniform size.

Another source of attrition, although not considered so important as cannibalism, was predation by dragonfly nymphs. These highly predacious larvae, which occurred commonly in the fry and assault-boat tanks, usually preyed on the smaller fry. Considerable effort was made to remove these nymphs. Chemical means of control (salt, potassium permanganate, and pyridylmercuric acetate, commonly called PMA) proved ineffective; dipnetting them individually seemed the most effective method.

SUMMARY AND CONCLUSIONS

This study evaluates the physical and biological feasibility of producing bait-size tilapia in tanks. Two facilities were used during the experiments. The first facility, or pilot plant, constructed on the grounds of the Bureau of Commercial Fisheries Biological Laboratory at Honolulu, Hawaii, was used from October 1956 to July 1958; the second, at the Kewalo Basin docksite, Honolulu, was used from August 1958 until September 1959. Results obtained at the pilot plant were of a preliminary and general nature, but aided in planning the more detailed experiments designed to examine factors associated with variations in reproduction and growth at the Kewalo plant.

Brood tanks at the pilot plant were stocked at the rate of 0.9 and 1.9 square feet of floor area per individual and with a sex ratio of 2 ♀ : 1 ♂. Stocking of the Kewalo tanks varied from 0.5 to 1.6 square feet of bottom area per individual, and the sex ratios (♀ : ♂) were 2 : 1, 3 : 1, 4 : 1, and 6 : 1.

Supplementary feeding of the tilapia included rice bran, chicken mash, alfalfa pellets, rabbit feed, and pelletized pond-fish feed and trout feed. Generally, for the adults pelletized feeds were much more satisfactory than finely divided mash and bran. Young fish were fed finely ground pondfish and trout feed.

Chemical analyses to determine concentrations of oxygen, free carbon dioxide, total bicarbonate and carbonate alkalinity, and hydrogen-ion were made routinely at weekly intervals to follow gross changes in the environment within the tanks.

Fry production at the pilot plant started in December 1956, approximately 9 weeks after the initial stocking. Nest-building activity was noted only after 3 to 4 inches of calcareous beach sand was placed in two of the brood tanks. Evidence of spawning on the bare floor, however, was noted when the one tank without sand was drained.

At both rearing plants, as the young emerged each day they were captured with a fine-meshed dipnet and counted. They were then placed in a fry tank and segregated by size in different compartments to prevent cannibalism.

Mortalities among the adults were attributable to factors such as handling, disease, asphyxiation, and possibly hydrogen sulfide poisoning. Highest mortality rates among the young were attributed to outbreaks of infectious disease and infestation by ectoparasites. Infestation by protozoan ectoparasites such as trichodinids and *Chilodon* spp. was rather easily controlled by chemical treat-

ment. Outbreaks of infectious pancreatic necrosis, believed to be caused by a virus, were not controlled by any of the methods tried. Strict sanitation, prevention of overcrowding in the fry-tank compartments, and periodic prophylactic treatments were found to be good control measures for preventing outbreaks of disease.

Several factors were found to affect fry production. The spawning rate was increased during the winter months by artificially raising the temperature of the water. Only a slight rise was necessary to increase spawning frequency, but prolonged constant high temperature seemed to have a detrimental effect.

A sex ratio of 3 ♀ : 1 ♂ resulted in the highest reproductive rate. An allotment of about 4.0 square feet of bottom area per male and 1.0 square foot per individual provided the most optimum conditions for courtship and spawning. Brood stocks fed high-quality feed had higher production per female than those fed low-quality feed. A significantly higher fry production occurred in brackish water (about 10 °/₀₀) than in fresh water.

The growth of young fish was influenced by environmental factors. Significantly faster growth rates were found among young reared in less crowded tanks than in crowded tanks. Young reared on high-quality feed also evinced a much faster growth rate than those fed low-quality feed. The growth of young fish in brackish water of a salinity of about 10 °/₀₀ was remarkably fast.

An investigation of cannibalism indicated that juveniles averaging 20.4 mm. (about 0.75 in.) can kill or consume fry up to 10 mm. (about 0.38 in.) in length, and juveniles averaging 64.4 mm. (about 2.5 in.) in length are able to kill or consume smaller juveniles up to a maximum size of 24.5 mm. (about 1 in.). Starved juveniles evinced a much more aggressive response than well-fed juveniles to fry introduced into their tanks.

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APPENDIX

APPENDIX TABLE 1.—*Oxygen concentrations (ml./l.) at the pilot plant, determined weekly, April 2, 1957–July 8, 1958*

Date	Zone time	Tank No. —			Assault-boat[1] tank No. —				Fry tank	Tap water
		1	2	3	1	2	3	4		
1957:										
Apr. 2	0900	0.75	3.87	4.61						4.29
9	1000	4.75	6.75	5.71						6.06
16	1000	2.67	5.80	3.81						6.08
23	1000	4.88	5.56	3.90						5.97
30	1000	3.72	5.30	4.80						5.32
May 7	1100	2.94	5.25	3.75						6.17
14	1000	0.77	2.56	2.87						6.09
21	1000	3.36	2.59	2.70						5.68
28	1000	3.33	3.64	3.34						6.36
June 4	1000	1.68	2.03	2.42						6.15
11	1000	3.16	2.78	2.70						6.08
19	1000	0.63	0.54	1.10						6.08
26	1000	1.12	0.54	1.56						6.08
July 2	1000	2.68	0.96	4.22						6.06
9	1000	3.58	3.30	3.76						6.48
16	0830	1.78	1.73	3.42		5.40	2.40	3.53		5.88
23	0830	3.78	3.34	5.40		5.19	1.90	3.69	1.05	6.12
31	1000	5.60	6.96	6.54	4.38	4.34	3.25	4.30	5.14	5.70
Aug. 6	0830	1.34		2.51	3.10	4.02	3.77	2.46	4.37	5.57
13	0830	1.30	2.76	1.40		3.66	3.59		3.57	5.84
22	1000	5.22	4.33	2.59	6.51	3.43	5.49		4.11	5.84
28	0830	0.62	1.95	1.40	5.14	4.12	4.84	4.52	4.64	5.91
Sept. 5	0830	1.81	3.04	3.33	5.64	4.00	5.72	4.70	4.11	5.64
10	0830	0.74	1.23	2.75	4.86	4.27	4.77	4.53	3.54	5.79
18	0830	1.18	0.92	1.39	4.86		2.96		2.77	5.68
25	0830	0.85	1.17	1.65	5.52	2.69			3.36	6.78
Oct. 3	0830	0.87	1.31	1.41	5.79	4.42	2.63		3.77	5.83
11	0830	0.56	0.85	3.13	5.42	3.85	2.11		4.20	5.84
16	0830	0.58	0.72	1.49	5.48	4.18	1.90	2.46	4.75	5.72
23	0830	0.85	1.35	1.55	4.57		1.56	1.05	3.38	6.01
30	0830	2.68	1.37	2.41	4.44	3.67	0.95	0.93	6.00	6.05
Nov. 6	0830	0.90	6.42	3.97	6.31	5.66	2.66	2.06	6.81	6.03
12	0800	1.17	0.78	1.84	4.36	2.77	0.74	0.73	3.00	5.99
20	0845	1.44	2.57	2.45	5.27	3.84	1.69	0.61	3.08	6.17
Dec. 3	1000	2.40	3.75	2.80	5.48	5.02	4.64		6.44	5.93
10	1000	4.22	6.34	2.14	5.72	5.18	4.54		5.82	5.92
20	1100	3.74	6.16	2.36						
26	0900	0.40	1.86	1.83	4.79			5.54		6.12
1958:										
Jan. 9	1300	3.24	7.93	2.46		5.95			6.97	6.22
16	1000	0.56	0.26	2.18		6.23			6.48	6.46
24	0815	0.38	0.90	2.42		5.77			5.76	5.71
Feb. 6	1300	4.20	3.13	5.21					6.96	6.21
14	1000	0.51	1.07	1.07					5.85	6.42
28	1300	5.65	6.74	2.42					7.04	6.09
May 26	0800	0.64	0.69	0.34					5.66	
June 12	0800	0.46	0.19	0.28						6.05
17	0830	1.60	0.97	0.38						5.80
24	0815	0.64	0.10	0.35						5.95
July 2	0815	1.26	1.15	0.06					5.45	
8	0800	1.15	0.91	0.85					5.46	

[1] Acquired June 1957.

APPENDIX TABLE 2.—*Oxygen concentrations in tanks 1 and 2 sampled hourly for 24 hours, at the pilot plant, November 12–13 1957*

Zone time	Tank 1 [1]		Tank 2 [2]		Cloud cover	Comments
	Oxygen (ml./l.)	Temperature (° F.)	Oxygen (ml./l.)	Temperature (° F.)		
0800	1.17	73.5	0.78	74.5	6/8	Sun clouded over.
0900	1.50	74.0	4.71	75.0	4/8	Tanks partly exposed to sunlight.
1000	2.00	75.0	5.57	76.0	3/8	Tanks fully exposed to sunlight.
1100	2.46	76.0	8.08	77.0	2/8	Do.
1200	2.83	77.5	10.46	78.5	1/8	Do.
1300	3.32	78.5	12.24	79.5	1/8	Tanks 1/4 shaded from sunlight.
1400	3.59	79.0	12.36	80.0	1/8	Tanks 1/2 shaded from sunlight.
1500	3.49	78.5	11.31	80.0	1/8	Tanks almost entirely shaded from sunlight.
1600	3.22	78.5	9.45	80.0	2/8	Tanks completely shaded from sunlight.
1700	3.01	78.0	8.21	79.0	2/8	Do.
1800	2.65	77.5	6.98	79.0	Dark	Dark.
1900	2.12	77.0	5.66	78.5	do	Do.
2000	1.82	76.5	4.99	76.0	do	Do.
2100	1.46	76.5	4.30	76.0	do	Do.
2200	1.24	76.0	3.84	76.0	do	Do.
2300	1.08	76.0	3.27	76.0	do	Do.
0000	0.94	75.5	3.06	76.5	do	Do.
0100	0.86	75.5	2.80	76.5	do	Do.
0200	0.69	75.5	2.56	76.5	do	Do.
0300	0.50	75.0	2.26	76.0	do	Do.
0400	0.46	74.5	2.00	75.5	do	Do.
0500	0.43	74.5	1.88	75.5	do	Do.
0600	0.38	74.0	1.54	75.0	do	Daylight visible at 0620.
0700	0.37	74.0	1.23	75.0	1/8	Sunlight visible.
0800	0.42	74.0	1.17	75.0	1/8	Tanks partly exposed to sunlight.
0815	0.48	74.0	1.33	75.0	1/8	Tanks almost all exposed to sunlight.

[1] Tank 1 was cleaned on Nov. 4, 1957 and the water was still relatively low in algae on Nov. 12 and 13.
[2] Tank 2 had a high concentration of algae (*Chlorella*).

APPENDIX TABLE 3A.—*Oxygen concentrations (ml./l.) observed in sex ratio-fish concentration experiment, August 27–November 26, 1958*

Date	Zone time	Tank 1	Tank 2	Tank 3	Tank 4	Tank 5	Tank 6	Tank 7	Tank 8	Tank 9	Tank 10	Tank 11	Tank 12
Aug. 27	0830	5.65	1.68	5.36	3.18	3.28	2.63	4.90	3.80	3.62	2.24	4.69	3.66
Sept. 4	0830	4.04									1.62		4.18
12	0815	1.53						3.57					1.83
19	0810	3.00									2.84		1.10
Oct. 2	0815				2.48		3.65		0.36				
9	0815	1.75								2.72	1.25		
16	0815				1.98	0.43							1.00
23	0800				0.80	1.54							0.81
30	0800				2.74	0.76							1.82
Nov. 6	0800	2.45						2.22					2.03
13	0800	1.58			0.81					1.16			
20	0800	3.90				0.30				1.54			
26	0800					1.44					1.06		2.87

APPENDIX TABLE 3B.—*Oxygen concentrations (ml./l.) observed in feeding experiment, August 27–November 26, 1958*

Date	Zone time	Tank 13	Tank 14	Tank 15	Tap water
Aug. 27	0830	1.17	1.94	1.04	
Sept. 4	0830	2.81			5.74
12	0815	1.09			
19	0810	2.31			
Oct. 2	0815		0.99		5.96
9	0815			1.68	5.56
16	0815		1.15		5.58
23	0800		0.86		6.00
30	0800			2.98	5.84
Nov. 6	0800			1.69	6.57
13	0800			0.97	5.96
20	0800		1.83		6.68
26	0800		1.45		6.30

APPENDIX TABLE 4.—*Oxygen concentrations (ml./l.) in tanks 13, 14, and 15 during heating experiment, January 16–August 27, 1959*

Date	Zone time	Tank 13	Tank 14 (with heating cable and cover)	Tank 15 (with heating cable only)	Tap water
Jan. 16	0815	6.69	0.80	4.72	5.96
23	0800	2.49	0.69	2.57	6.03
28	0800	1.51	0.78	0.83	5.99
Feb. 5	0800	3.11	3.04	4.94	5.76
12	0800	0.91	0.95	1.17	5.82
19	0815	3.97	3.59	3.09	6.32
26	0800	5.32	4.14	4.39	6.53
Mar. 5	0805	5.06	1.86	5.09	6.00
12	0800	4.83	2.11	4.05	4.89
19	0800	4.49	3.56	4.84	5.96
26	0800	3.01	1.37	4.87	7.74
Apr. 2	0800	3.49	1.64	2.86	5.95
9	0800	2.96	5.58	2.04	6.30
16	0800	1.23	2.77	1.53	6.30
23	0800	1.72	2.63	3.28	6.28
30	0810	1.76	2.84	2.27	6.20
May 7	0810	3.32	2.27	2.98	5.98
14	0810	2.54	3.72	4.05	6.10
21	0800	2.46	2.95	3.01	6.06
28	0810	3.01	3.54	4.46	6.10
June 4	0815	4.20	4.43	4.55	6.12
11	0815	4.45	4.36	4.46	5.98
18	0810	3.54	3.79	3.93	5.99
25	0800	4.29	3.99	4.99	5.85
July 2	0800	5.45	2.83	5.39	6.18
9	0800	4.35	2.40	2.92	5.99
16	0800	4.20	1.31	3.55	6.10
23	0800	3.06	2.63	3.34	5.96
30	0800	2.53	1.86	3.40	5.

APPENDIX TABLE 4.—*Oxygen concentrations (ml./l.) in tanks 13, 14, and 15 during heating experiment, January 16–August 27, 1959*—Continued

Date	Zone time	Tank 13	Tank 14 (with heating cable and cover)	Tank 15 (with heating cable only)	Tap water
Aug. 6	0800	2.08	1.51	2.69	6.26
13	0800	4.92	0.84	1.60	5.98
20	0800	4.42	1.53	3.00	5.70
27	0800	3.71	0.89	1.18	5.97

APPENDIX TABLE 5.—*Oxygen concentrations (ml./l.) in brackish-water and fresh-water tanks, during salinity-spawning experiment, August 6–September 24, 1959*

Date	Zone time	Tank 1 (braekish water)	Tank 5 (fresh water)	Tap water
Aug. 6	0800	4.95	2.63	6.26
13	0800	4.16	2.08	5.98
20	0800	3.21	1.13	5.70
27	0800	3.22	1.42	5.97
Sept. 3	0800	1.82	0.61	7.25
10	0800	1.18	1.44	5.56
17	0815	4.11	1.28	6.05
24	0800	0.90	2.34	6.34

APPENDIX TABLE 6A.—*Hydrogen-ion (pH) values observed in sex ratio-fish concentration experiment, October 2–November 26, 1958*

Date	Zone time	Tank 1	Tank 2	Tank 3	Tank 4	Tank 5	Tank 6	Tank 7	Tank 8	Tank 9	Tank 10	Tank 11	Tank 12
Oct. 2	0800	7.7	8.1	8.2	7.9	8.6	7.7	8.6	7.3	7.7	8.3	7.9	7.9
9	0800	7.9	7.7	7.7	8.5	7.7	7.3	7.6	7.6	7.7	7.5	7.4	7.7
16	0800	8.8	8.1	7.7	8.7	7.4	7.7	7.5	7.6	7.3	7.6	7.5	7.6
23	0800	7.9	7.4	7.4	7.4	7.8	7.4	7.8	7.5	7.3	7.5	7.5	7.3
30	0800	>8.8	----	----	----	----	>8.8	>8.8	----	----	----	----	8.1
Nov. 6	0800	>8.8	----	----	----	8.4	----	----	----	7.9	----	----	8.0
20	0800	8.7	8.3	8.7	8.8	7.9	>8.8	>8.8	>8.8	8.7	8.5	8.7	8.1
26	0800	8.6	7.7	7.9	>8.8	7.4	7.9	8.7	8.1	7.7	7.6	8.4	8.7

APPENDIX TABLE 6B.—*Hydrogen-ion (pH) values observed in feeding experiment, October 2–November 26, 1958*

Date	Zone time	Tank 13	Tank 14	Tank 15	Tap water
Oct. 2	0800	8.6	7.4	7.7	8.0
9	0800	8.7	7.7	7.7	8.2
16	0800	8.7	7.6	8.1	8.2
23	0800	7.7	7.5	7.5	8.3
30	0800	----	8.3	----	----
Nov. 6	0800	----	7.7	----	----
20	0800	8.4	8.1	8.2	8.1
26	0800	8.1	7.6	7.9	----

APPENDIX TABLE 7.—*Hydrogen-ion (pH) values during heating experiment, determined weekly, January 16–August 27, 1959*

Date	Zone time	Tank 13 (control)	Tank 14 (with heating cable and cover)	Tank 15 (with heating cable only)	Tap water
Jan. 16	0815	8.7	7.7	8.6	
23	0800	8.4	7.8	8.3	
28	0800	7.8	7.5	7.9	8.1
Feb. 5	0800	8.8	8.1	8.8	8.1
12	0800	7.4	7.4	7.6	8.1
19	0815	7.6	7.6	8.8	
26	0800	7.9	8.0	8.4	7.9
Mar. 5	0805	7.7	7.5	7.9	8.2
12	0800	8.0	7.5	8.0	8.1
19	0800	7.9	7.7	8.1	8.1
26	0800	7.7	7.5	7.9	8.3
Apr. 2	0800	7.7	7.5	7.9	8.3
9	0800	7.7	7.9	8.1	8.1
16	0800		7.7		8.3
23	0800	7.7	7.4	7.7	8.1
30	0810	8.4	7.9	8.3	8.1
May 7	0810	7.9	7.8		8.1
14	0810	8.1	8.1	8.7	8.3
21	0800	7.9		8.4	8.1
28	0810	7.7	7.9	8.1	7.9
June 4	0815	7.9	8.1	8.5	7.9
11	0815	8.2	8.1	8.2	7.9
18	0810	8.1	8.1	8.1	7.9
25	0800	8.1	7.7	7.9	8.1
July 2	0800	7.8	7.5	7.7	7.9
9	0800	8.1	7.6	7.4	7.9
16	0800	8.3	7.4	7.5	7.9
23	0800	7.5	7.4	7.5	7.9
30	0800	7.8	7.5	7.7	7.9

APPENDIX TABLE 7.—*Hydrogen-ion (pH) values during heating experiment, determined weekly, January 16–August 27, 1959*—Continued

Date	Zone time	Tank 13 (control)	Tank 14 (with heating cable and cover)	Tank 15 (with heating cable only)	Tap water
Aug. 6	0800	7.3	7.3	7.4	8.2
13	0800	7.7	7.3	7.3	7.9
20	0800	7.8	7.3	7.5	8.1
27	0800	7.6	7.3	7.3	7.9

APPENDIX TABLE 8.—*Hydrogen-ion (pH) values in brackish- and fresh-water tanks during salinity-spawning experiment, August 6–September 24, 1959*

Date	Zone time	Tank 1 (brackish water)	Tank 5 (fresh water)	Tap water
Aug. 6	0800	8.3	7.7	8.2
13	0800	8.2	8.3	7.9
20	0800	8.0	8.2	8.1
27	0800	7.7	8.1	7.9
Sept. 3	0800	7.7	7.7	7.9
10	0800	7.6	7.9	8.0
17	0815	7.5	8.1	8.0
24	0800	7.6	8.1	7.9

APPENDIX TABLE 9.—*Free carbon dioxide, bicarbonate, and normal carbonate in control and heated tanks during heating experiment and in the fry tank, determined weekly, February 26–August 27, 1959*

[In parts per million]

Date	Zone time	Tank 13 (control)			Tank 14 (heated and covered)			Tank 15 (heated)			Fry tank		
		Free CO_2	Carbonate	Bicarbonate	Free CO_2	Carbonate	Bicarbonate	Free CO_2	Carbonate	Bicarbonate	Free CO_2	Carbonate	Bicarbonate
Feb. 26	0800		37.6	115.8									
Mar. 5	0805	0.0	40.8	56.4	0.0			0.0	63.8	15.2	0.0	42.6	23.5
12	0800	0.0	7.4	112.6				0.0	13.0	75.3	0.0	32.6	30.1
19	0800	0.0	14.6	111.4	3.8	0.0	136.2	0.0	3.0	93.6	0.0	19.4	37.4
26	0800	8.0	0.0	154.1	6.9	0.0	122.3	5.8	0.0	115.8	0.0	11.4	52.7
Apr. 2	0800	7.3	0.0	181.7	5.9	0.0	141.6	0.0	5.4	115.4	0.0	3.6	58.9
9	0800	5.5	0.0	173.3	2.0	0.0	65.2	0.0	3.6	104.8	0.0	9.8	60.7
16	0800		0.0	146.4	6.7	0.0	83.4		0.0	123.7	0.0	38.8	23.7
23	0800	5.4	0.0	147.0	6.8	0.0	86.3						
30	0810	0.0	2.0	118.4	3.7	0.0	85.5	0.0		130.5	0.0	12.0	57.0
May 7	0810	2.9	0.0	111.0	3.8	0.0	92.0		0.0	79.3	0.0	7.6	56.7
14	0810	3.9	0.0	117.0	2.7	0.0	85.4	0.0	13.4	59.1	0.0	17.2	42.8
21	0810	5.7	0.0	131.5		0.0	81.0	0.0		82.3	0.0	7.8	55.7
28	0810	4.1	0.0	123.5	2.6	0.0	81.4	0.0		76.6	0.0	29.0	34.0
June 4	0815	3.8	0.0	115.9	0.0		79.1	0.0	12.2	57.2	0.0	2.4	62.6
11	0815	0.0						0.0	3.8	76.7	0.0	7.4	62.9
18	0810	0.0	26.0	84.3				0.0	10.8	83.8	0.0	16.0	57.7
25	0800	0.0			4.1	0.0	104.3	0.0	16.2	85.0	0.0	32.0	57.1
July 2	0800	1.2	0.0	73.1	1.4	0.0	116.6	2.2	0.0	77.2	0.0	32.2	46.3
9	0800	0.0		86.5	4.9	0.0	108.0	4.7	0.0	111.7	0.0	15.4	58.3
16	0800	0.0	11.6	74.1	5.8	0.0	128.3	3.8	0.0	107.9	0.0	11.2	60.6
23	0800	1.7	0.0	83.5	5.5	0.0	124.7	4.8	0.0	117.4	2.3	0.0	81.4
30	0800	0.0	24.8	72.8	7.5	0.0	121.4	3.4	0.0	109.2	0.0	36.1	48.8
Aug. 6	0800	6.5	0.0	180.5	8.5	0.0	117.3	5.2	0.0	115.9	1.2	0.0	76.5
13	0800	1.2	0.0	97.4	11.5	0.0	133.4	6.9	0.0	125.3	2.4	0.0	74.6
20	0800	0.0	17.0	102.8	10.0	0.0	135.0	7.0	0.0	110.7	0.0	66.2	20.6
27	0800	0.0	18.8	97.3	13.3	0.0	140.0	12.7	0.0	149.1	0.0	22.0	59.2

APPENDIX TABLE 10.—*Free carbon dioxide, bicarbonate, and normal carbonate in brackish- and fresh-water tanks during salinity-spawning experiment, August 6–September 24, 1959*

[In parts per million]

Date	Zone time	Tank 1 (brackish water)			Tank 5 (fresh water)		
		Free CO_2	Carbonate	Bicarbonate	Free CO_2	Carbonate	Bicarbonate
Aug. 6	0800	1.7	0.0	94.4	3.5	0.0	111.8
13	0800	0.0	19.1	69.3	0.0	30.6	65.0
20	0800	0.0	14.4	86.7	0.0	24.2	80.1
27	0800	2.6	0.0	123.4	0.0	39.0	71.0
Sept. 3	0800	4.0	0.0	183.3	0.0	80.6	36.3
10	0800	16.2	0.0	188.5	0.0	32.2	81.8
17	0815	8.0	0.0	188.1	0.0	40.0	76.3
24	0800	13.6	0.0	214.0	0.0	54.4	45.3

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GROWTH OF THE ADULT MALE KING CRAB *PARALITHODES CAMTSCHATICA* (TILESIUS)

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A request for study of the southeastern Bering Sea king crab (*Paralithodes camtschatica* (Tilesius)) stock was made to the International North Pacific Fisheries Commission by the United States Government in February 1954 in accordance with Article III, Section 1, (c), (i) of the International Convention for the High Seas Fisheries of the North Pacific Ocean, for the purpose of ". . . determining need for joint conservation measures of the Contracting Parties conducting substantial exploitation of that stock." (The Contracting Parties in this instance are Japan and the United States.)

The Bureau of Commercial Fisheries Biological Laboratory in Seattle, Washington (then Pacific Salmon Investigations) was assigned this study for the United States. Investigations began in 1954, with emphasis on factors governing yield, e.g., growth recruitment, mortality, and abundance.

In compliance with part of the request, this report presents an estimate of growth of adult male king crabs of the eastern Bering Sea and describes methods employed. Although growth of all king crabs is being studied, that of adult males has been given priority, because the commercial fisheries are concentrated on them and need for their conservation must, therefore, be determined first.

The authors are indebted to many individuals who contributed toward this study. The Nippon Suisan Company, J. E. Shields Company, and Wakefield's Deep Sea Trawlers, Inc. cooperated in recovering tagged crabs; Seiwa Kawasaki, biologist of the Japan Fisheries Agency, recorded very complete tag recovery information, a major contribution; F. C. Cleaver and R. A. Fredin, advised and aided us throughout the study, and T. H. Butler, A. E. Peterson, and W. F. Thompson provided helpful comments concerning the treatment of data.

BACKGROUND INFORMATION

The king crab, being a decapod crustacean, has a typical rigid exoskeleton which prevents a change in carapace dimensions except at molting. Consequently the growth of an individual consists of a series of steps, the frequency of which decreases as the animal increases in age or size. An exception is the mature female king crab, which molts annually prior to egg extrusion, often without appreciable increase in carapace dimensions.

At molting the entire exoskeleton is cast along with the mouth and stomach parts, gills, tendons, and other structures of ectodermal origin. Since all hard parts of the body are lost, determination of growth must be achieved by means other than those applicable to animal forms which have permanent records of seasonal growth such as may be found on the scales of fish.

Several methods have been used to study growth of king crabs. Most of the studies were made by Japanese scientists and depend upon one or combinations of three basic types of data: Growth increment per molt and frequency of molt; size-frequency distributions from 1 year which show modes that are indicative of year classes; and size-frequency distribution data taken in successive years to observe the progression of weak or dominant year groups through the years.

Wang (1937) described growth rates for young crabs, as interpreted from an examination of modes in size-frequency distribution and for the older crabs by following the progression of modes in size-frequency data collected in 3 successive years. Marukawa (1933) studied live tank-reared crabs and observed growth per molt and frequency of molt in conjunction with size-

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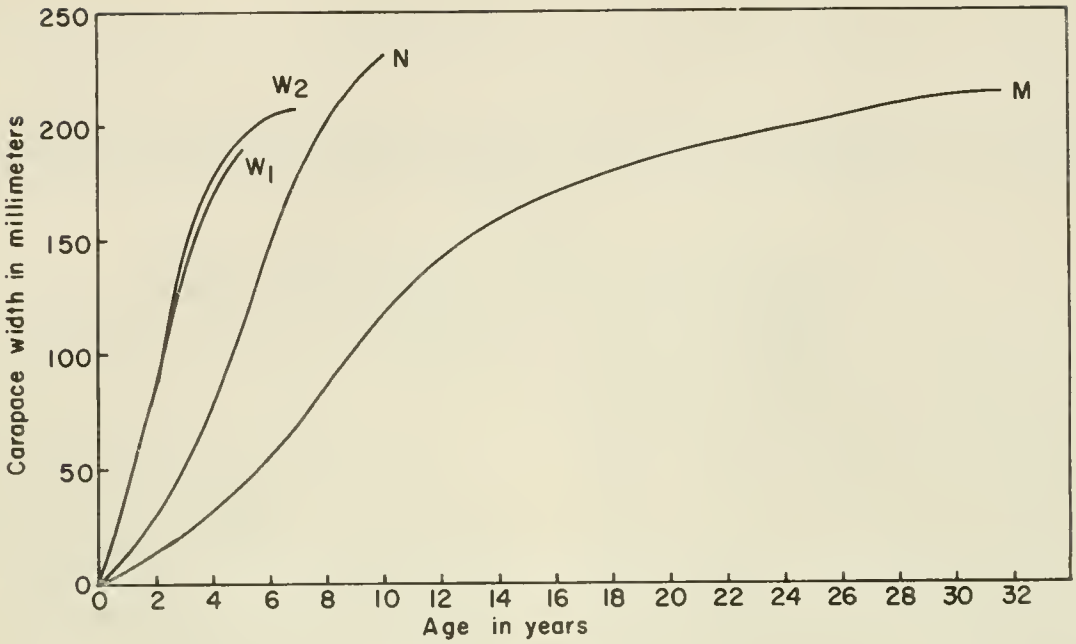

FIGURE 1.—King crab growth curves from published results. Curves W_1 and W_2 derived from Wang (1937) for crabs from Northern Hokkaido and Sakhalin, respectively; curve N derived from Nakazawa (1912); and curve M from Marukawa (1933).

frequency distributions. Nakazawa (1912) estimated growth of king crabs by combining data from his studies on king crab with published information on the frequency of molt and growth rate of *Homarus americanus* and *Cancer pagurus*. The growth curves described by the above investigators are presented in figure 1.[1]

Wide differences in growth rates are indicated, and though the difference may in part be due to geographic separation, it appears that there may be some errors in interpretation.

Wang (1937), graphically presents a size-frequency distribution which shows a mode at 45 mm., a second at 85 mm., and others centered at 115 mm., 135 mm., and 155 mm. From other size-frequency distribution data collected in 3 successive years, he observes weak and dominant groups progressing from 135 mm. to 160 or 165 mm. and then to 185 mm. Wang combines the two sets of data and interprets the first two modes in the size-frequency distribution to be indicative of sizes at ages 1 and 2, and then from the modal progression, the sizes at ages 3, 4, and 5, to be 135 mm., 165 mm., and 185 mm., respectively. Wang apparently does not interpret the increased frequency of 115-mm. crabs as representing a year class. Unfortunately, sufficient data are not presented to permit examination of his frequency distribution, and reasons are not given for excluding the 115-mm. group which is quite evident in the size-frequency distribution presented.

Wang's assignment of age 1 to the first mode in his sample (45 mm.) is not consistent with the findings of other researchers. Marukawa and Nakazawa both describe 1-year-old crabs to be of about 7 and 8 mm., respectively. Also, the Fisheries Agency of Japan (1958) reports that 3,084 juvenile crabs, ranging in size from 6 to 15 mm. in carapace length with a mean size of 9 mm. (carapace width, 8 mm.), were collected in the eastern Bering Sea in late May and early June of 1957. Since hatching in the eastern Bering Sea occurs in April and May and it is generally agreed that there is about a 10-week period of larval life be-

[1] Marukawa, Nakazawa, and Wang's results were presented in terms of carapace width, and are so shown in figure 1. However, most if not all king crab investigators are presently using carapace length measurements, since this dimension is more definite and the points of measurement are more resistant to flexing when measuring calipers are applied. The conversion from width to length for male king crabs may be made by the formula: carapace length = .14 + 0.925 (carapace width), for sizes less than 95 mm. in carapace width; and for sizes greater than 95 mm. the formula is: carapace length = 1.84 + 0.744 (carapace width). These relations were calculated from length-width measurements of eastern Bering Sea king crabs.

fore the adult form occurs at 2 mm., it is unlikely that these 9 mm. crabs are of 0-age class, but are probably 1 year old.

Further, it is our belief that another year group between 8 mm. and 45 mm. is to be expected. In a study [2] of the growth of small crabs in Unalaska Bay, Alaska, we sampled at 4-month intervals from May 1958 through May 1959. By observing the progression of modes in these samples, we concluded that crabs sampled in May of 1958 were in their second year at a carapace width of 11 to 12 mm. and were in their third year at a carapace width of 37 mm. According to our data, a crab near the end of its third year of life would be approximately 45 mm. or larger. If geographic variation in growth is not great, it seems reasonable to expect that if crabs near Japan are about 8 mm. at age 1, then at age 2 they would be less than 37 mm., and 45-mm. crabs may be 3 years of age rather than 1-year-old as postulated by Wang. It would then appear that Wang's curve may be shifted 2 years to the right. Also the inclusion of another year group at 115 mm., as noted in Wang's size-frequency distribution, would tend to decrease the slope beyond 85 mm.

Marukawa (1933), in his comprehensive and informative paper on *Paralithodes*, presents a discussion on growth, including the curve shown in figure 1, in which males reach a maximum carapace width of 216 mm. in 31 years. A review of Marukawa's methods and results is presented by McKay and Weymouth (1935), who point out that the early modes in Marukawa's size-frequency data probably represent instars rather than year classes, and that later modes most likely indicate chance irregularities. We generally agree with the reviewers. Marukawa's size-frequency distributions of smaller crabs show modes at 7, 17, 25, 34, 42, and 53 mm., which he interprets as being year classes. As discussed in the previous paragraph, progression of modes in a series of size frequencies taken throughout a year indicates greater spacing between year classes than are shown in Marukawa's size distribution. Sato (1958), also points out that the 17, 34, and 42 mm. modes in Marukawa's frequency curve can be considered as instars. That modes in the larger sizes are due to chance irregularities is suspected, since our observations of growth increments resulting from one molt would span from 3 to 6 modes. Thus, if some of the early modes were considered instars rather than year classes, the lower portion of Marukawa's curve would be steeper and would shift the remainder of the curve to the left. Consideration of fewer age classes in the larger sizes would also steepen the curve, and it would approach maximum size more rapidly.

Nakazawa (1912) presented information that enabled construction of the curve shown in figure 1, but unfortunately he did not include the data upon which his annual growth increments were based. His curve, however, is intermediate between Wang's (1937), whose growth rate appears too rapid, and that of Marukawa's (1933) which appears too slow. Other investigator's results of growth studies have been examined but were not included, since sufficient data were not presented to enable constructing curves.

The reports examined and the curves presented in figure 1 show wide differences that, as stated earlier, seem to be mainly due to errors in interpretation, but may, in part, be due to actual differences in growth demonstrating the difficulties in estimating growth of king crabs.

The growth studies to be discussed in the remainder of this report pertain to the eastern Bering Sea king crab. Although sexual maturity appears to be attained from 85–95 mm., the term adult used in this report includes all crabs larger than 80 mm. in carapace length. Determination of growth for the smaller sizes is based on modal progressions in size-frequency distributions, since modes are fairly well defined and little is known of growth per molt and molting frequency in these sizes. In the larger sizes, year classes tend to overlap due to nonmolting crabs, and modes when evident are probably made up of various year classes. For this situation a method was developed which is dependent upon a composite of the amount of growth observed in tagged crabs and the proportions observed to molt in any particular year. The resulting growth curve for the larger sizes, therefore, takes into consideration both molting and nonmolting crabs.

[2] The results of this study are described briefly in a paper submitted to the International North Pacific Fisheries Commission for inclusion in the 1959 Annual Report.

SOURCES OF DATA

Each summer since 1955, a commercial fishing vessel has been chartered to otter trawl for samples at predesignated stations 20 miles apart. The stations sampled by year are represented in figure 2.

The gear used each year was similar to that described by Greenwood (1958). This trawl is commonly called a "400 eastern type."

At each station all crabs caught were measured to the nearest millimeter, shell conditions were noted, and males were tagged and released. Two measurements were taken. Length of carapace was measured from the posterior margin of the orbit of the right eye to the midpoint of the posterior margin of the carapace. Greatest width of the carapace between spines was also measured as a check on accuracy of length measurement since a definite relationship exists between length and width.

We recorded four shell conditions, soft, new, old, and very old, which are subjective classifications of the length of time since molt. The principal basis of classification are scratches and discolorations of the ventral basal segments of the appendages. A soft exoskeleton is indicative of a crab which has just molted, since after approximately 1 week the shell becomes firm and resists flexing. New-shell crabs have hard exoskeletons, the ventral surfaces of which are white and unscratched, and are presumed to have molted during the winter or spring immediately preceding the sampling period. Crabs with yellowish ventral exoskeletons and multiple darkly stained scratches are classified as old-shells and are judged not to have molted for one or more years. The very-old-shell condition is an extension of the old-shell and is characterized by an almost black ventral exoskeleton and dense growth of fouling organisms. The time since last molting is not well

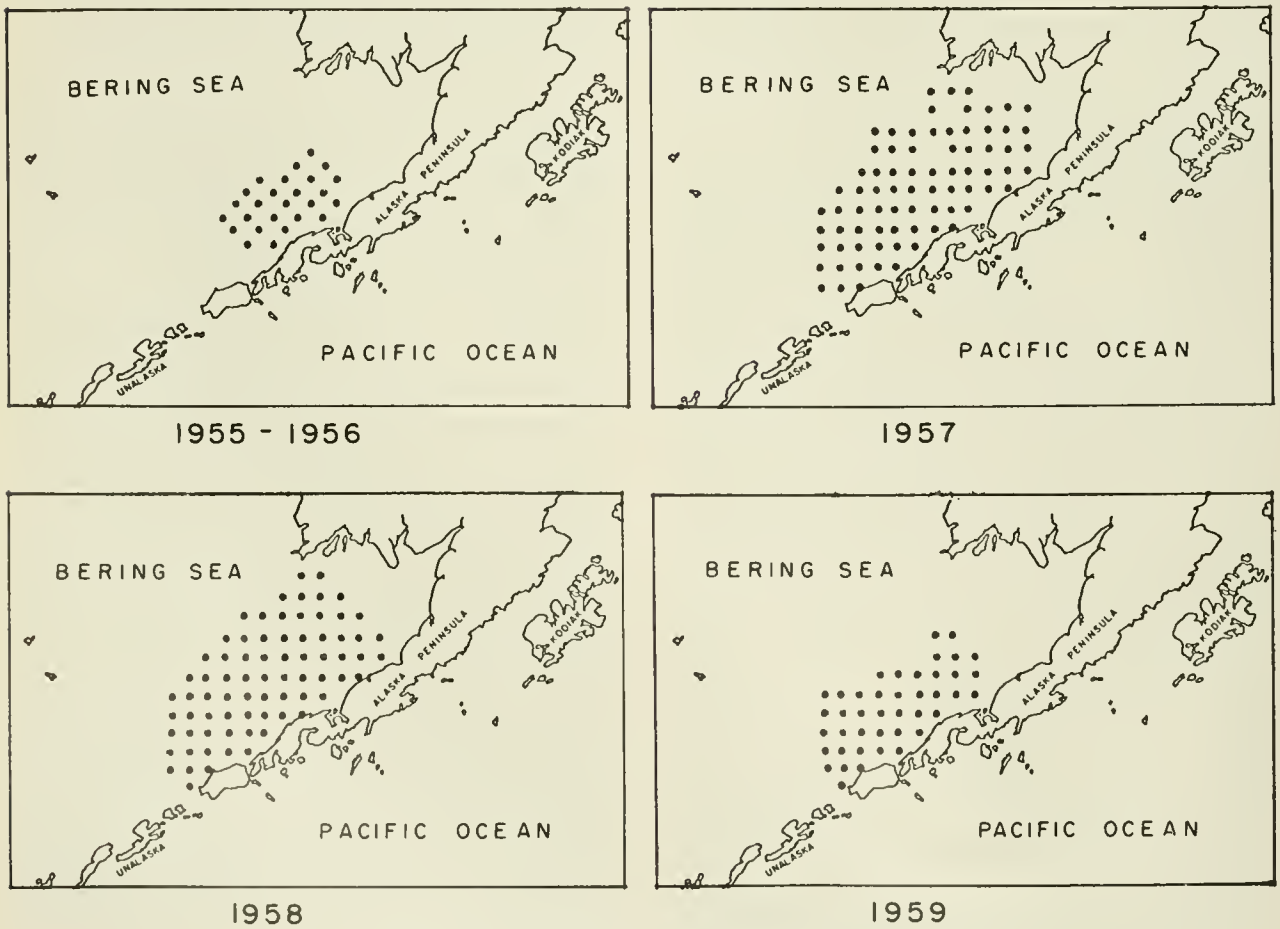

FIGURE 2.—King crab sampling stations for the years 1955 through 1959.

defined for the very-old-shell condition, but is believed to be noticeable in the second year after last molt. Individual fouling organisms which settle on the shell have not been considered as a measure of time since molting because the life cycle, such as time of setting and growth of these organisms in the Bering Sea is not known and would demand a separate study.

Shell conditions are the basis of determining molting frequency, and for the purpose of growth we are interested in those that molted in the current year and those that did not. In the remainder of this report soft and new-shell conditions are grouped as new-shell and refer to crabs that have molted in the current year, while old- and very-old-shell conditions are grouped as old-shell and refer to crabs which have not molted during the current year.

Since initiation of investigations in 1954, crabs have been tagged with either a Petersen disc-type tag on a leg or through the carapace, or with a spaghetti-type tag through the muscular isthmus between the posterior margin of the carapace and the abdominal region. Since Petersen disc-type tags are probably lost at molting, analysis of growth from tagged crab data has been restricted to recoveries of spaghetti-type tags which remain attached through molt.

Of 23,826 male crabs released with spaghetti-type tags in years 1955 through 1959, 1,103 have been recovered, of which 1,017 were returned with complete measurement data. Changes in sizes indicating growth were observed in 325 recoveries.

ADEQUACY OF DATA

Two population properties are assumed in this report. They are: (1) the growth of tagged individuals and the size frequency distribution samples are representative of the population, and (2) the same population is sampled each year. Support for these assumptions is provided from examination of our field observations which show: tagged crabs mix uniformly with the untagged crabs throughout the fishing area; repetitive sampling performed in 1956 and again in 1958 resulted in similar size-frequency distributions and percentages of shell conditions within each year; tagged crabs continue to be taken in successive years after release, and only in the Bering Sea. In addition, the sampling areas, particularly since 1957, are believed to include the major distribution of this population, since explorations by the United States Fish and Wildlife Service in 1949 (Ellson, Powell, and Hildebrand, 1950) and by the Japanese in 1957 (Fisheries Agency of Japan, 1958) revealed very few *Paralithodes camtschatica* in adjacent areas of the eastern Bering Sea.

In subsequent discussions, it will be evident that the 1957 data are anomolous with other years. The samples included fewer molters in the population, thus reducing the proportion of molting to nonmolting crabs. Examination of this feature shows that the 1957 data were collected later in the summer than in any of the other years. It is therefore possible that changes in distribution associated with this time period may affect the availability of new-shell crabs. That only new-shell crabs are affected is suspected by examination of all data which shows that the abundance of old-shell crabs appear relatively unchanged regardless of the time of sampling.

There is general agreement in published reports that male crabs larger than 110 mm. in carapace length, molt no more than once annually. From a study of shell conditions, Vinogradov (1945) established that the majority of the larger males molt once every 2 years. Also our records show that several tagged crabs were returned after 3 years with no evidence of molting.

The Fishery Market News (1942), Wallace, Pertuit, and Hvatum (1949) and discussions with fishermen indicate that the adult male king crab molting period and growth occur in late winter or early spring in the eastern Bering Sea. Our observations aboard chartered vessels show that soft-shell male crabs were caught only in May, and these have numbered one-tenth of 1 percent of the total number of males sampled. No male crabs in the molting or postmolting stages have been found in the summer and late fall surveys. Since growth takes place before our sampling periods, and there is no noticeable change in size-frequency distribution or shell-condition proportions during the sampling season, the crabs taken may be considered as representing an instantaneous sample.

The relation between time of molting and our period of sampling is an important part in differentiating, through the use of shell condition, the

crabs that molted during the current year from those that did not molt. The crabs that molted in the winter and early spring have had their shells no more than 6 months at the time of summer sampling, whereas those not molting have had their shells not less than 1 year. Although shell condition is a subjective classification, the difference in discoloration and marking of the exoskeleton is distinct.

Confidence in the ability to distinguish between the current year molters and those that molted in the previous year may be shown by an examination of shell-condition classifications of tagged crabs, recorded at release and again at recovery. The bulk of the recoveries and the classifications, were made aboard the Japanese mothership by a biologist following, for the most part, our written description of the various shell conditions. Excluding all tagged crab recoveries showing changes in length measurements, and therefore indicative of having molted, there were 595 tag returns with shell-condition data available for study. Table 1 shows the shell conditions recorded at release and recovery of the crabs and their periods of freedom.

Of the 417 recoveries of new-shell releases, one recovered after a year of freedom was classified as new-shell, and by our criteria of shell conditions is considered in error. An additional six were classified as new-old, indicating some doubt. The six doubtful cases were recorded in 1956, and after the 1957 season the definitions of the shell conditions were made more explicit. Of the old-shell releases, two recoveries within the year of release were classified as new shells on recovery and are considered misclassified. The amount of error in classification appears to be no more than 1.5 percent and may be as low as 0.5 percent if the six doubtful cases are not included.

TABLE 1.—*Shell condition classification at recovery of nonmolting tagged crabs*

Shell condition at release	Shell condition at recovery	Periods of freedom			
		Within year	After 1 year	After 2 years	After 3 years
New-shell	New	[1] 25	1	0	0
	Old	0	306	76	3
Old-shell	New	2	0	0	
	Old	72	82	22	

[1] Six additional crabs were recovered but classified as new-old and are not included.

The amount of growth per molt is determined by an examination of the tagged crab measurement data that were taken at release and again at recovery. Preliminary analysis of the relation of width and length of tagged crabs indicated some measurement error. Therefore, width on length regression and a 99 percent confidence interval around this regression were calculated from a random sample of 744 crabs. All tag recoveries where measurements fell beyond the interval were not considered in the analysis. A few recoveries were also discarded due to illogical length to shell condition relations, for example, an increase in carapace length inconsistent with a logical change in shell condition.

In order to determine the range of measurement error, we examined 128 within-season tag recovery measurements (appendix table 2) reasoning that variations in measurements for this group must result from error or bias. Plotting the deviations of recovery from release measurements shows that 99 percent of the deviations lie between plus and minus 4.4 mm. This is shown graphically by the shaded histogram in figure 3.

All tagged crabs, that measured 5 mm. or more larger when recovered, and which had a corresponding increase in width, are considered to represent crabs that grew during their periods of freedom. The deviations of the lengths at recovery from the lengths at release for 325 male crabs depicting growth are shown by the unshaded histogram in figure 3. Considering the shell condition and the length of time at liberty, 15 crabs with length increments greater than 23 mm. were considered to have molted at least twice, and therefore are not used in the analysis.

GROWTH BY SIZE FREQUENCIES

Length measurements of all male king crabs taken during station pattern sampling each year since 1955 (Appendix table 1) were smoothed by a moving average of three; the resulting numbers at each millimeter of length were expressed as percentages of each year's total. Percentages were used to compensate for varying numbers between years. To emphasize the dominant size groups and their progressions, the percentage deviation of each year's size frequency distribution from the 1955 through 1959 mean distribution was calculated. The resulting yearly positive and negative deviations are plotted on figure 4. Examination

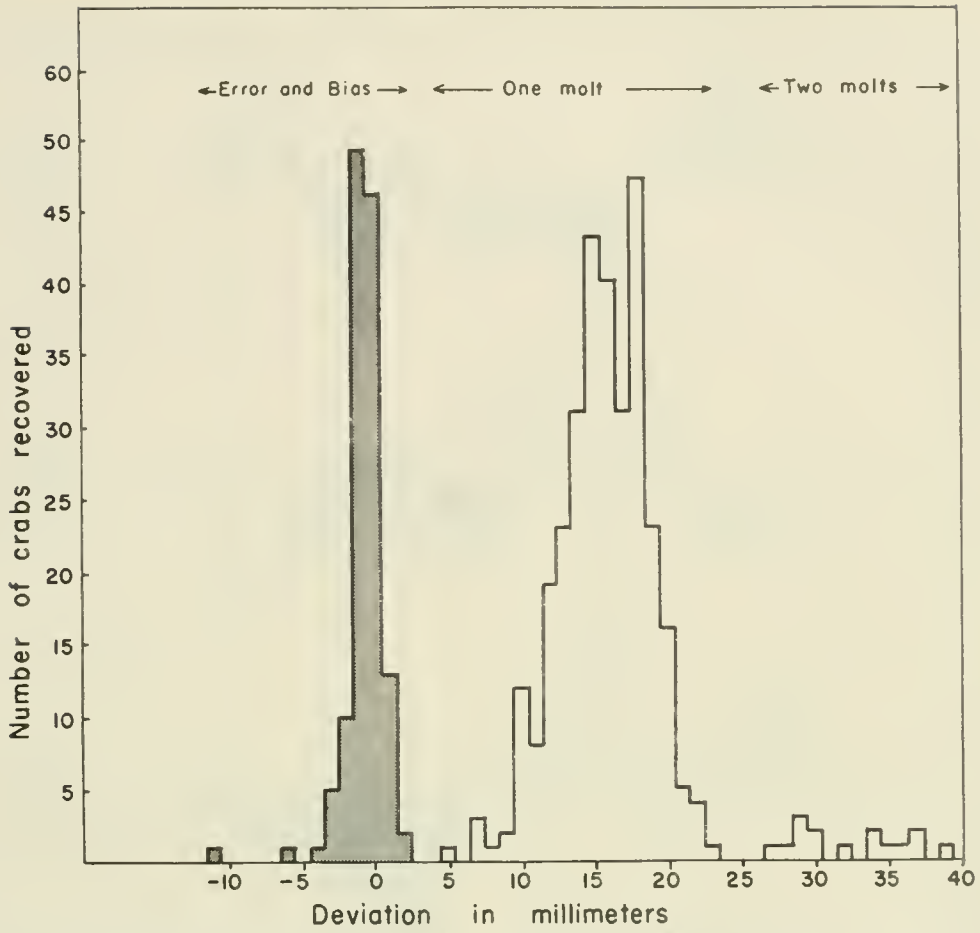

FIGURE 3.—Deviations of carapace length recovery measurements from release measurements. The shaded histogram represents 128 within-year tag recoveries. The unshaded histogram represents 325 tag recoveries showing growth.

of these deviations shows the presence and progression of at least two dominant size groups and one deficient size group. Since the juvenile crab studies have not progressed sufficiently to allow assignments of ages to the size groups represented, we have considered the size increase in relation to the time of entry into the sample of each dominant and weak group. These groups are designated for reference as A, B, and C.

TABLE 2.—*Range and mean size by year for size groups A, B, and C in figure 4*

Year	Size (mm.)					
	Group A		Group B		Group C	
	Range	Mean	Range	Mean	Range	Mean
1955	74–100	84.7				
1956	90–111	101.6	66–89	80.0		
1957	101–121	111.7	90–100	94.2	64–89	77.4
1958	122–141	131.7	101–121	111.3	84–100	92.3
1959	134–174	152.5	111–129	119.5	106–108	107.3

Dominant group A, shown first in the 1955 distribution, advances through the successive years to 1959 where it appears to include a rather wide range of sizes. Group B, which is characterized by a scarcity of crabs, is observed to progress from 1956 through 1959. Dominant size group C first became evident in 1957 and appears to be reduced after 2 years' progression. The reduction of group C is, in part, due to the method of using deviations from a mean, in which the strength of one size group, such as indicated by A in 1956 and 1957, may affect the plotted strength of another.

In order to present more clearly the progressions of these groups, the range and mean lengths were calculated, and are listed in table 2. In figure 5, the progressions of mean values of each group are plotted on years after first entry in the samples. Also included is the mean progression

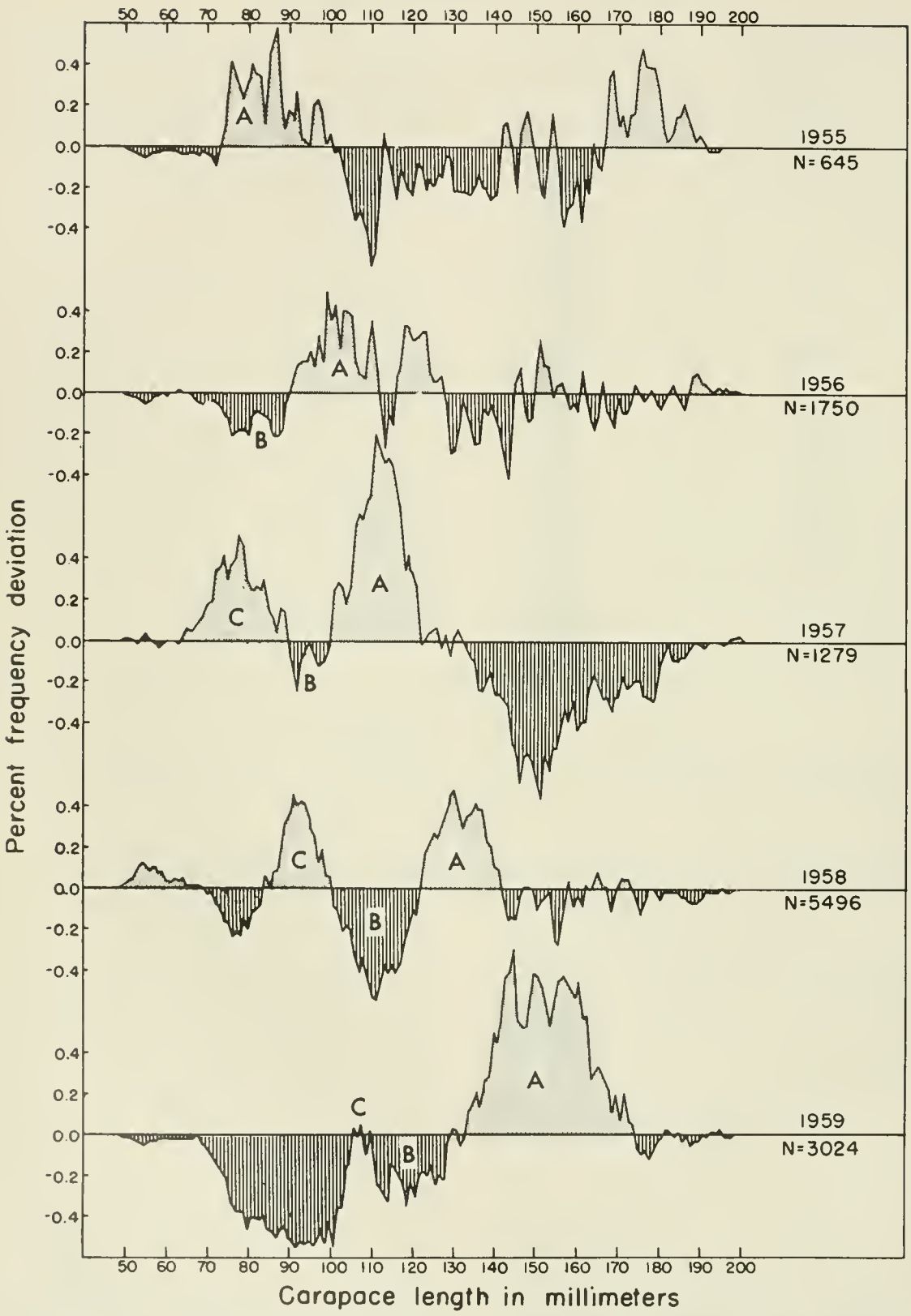

FIGURE 4.—Annual deviation from the 1955 through 1959 average size frequency expressed in percentage and smoothed.

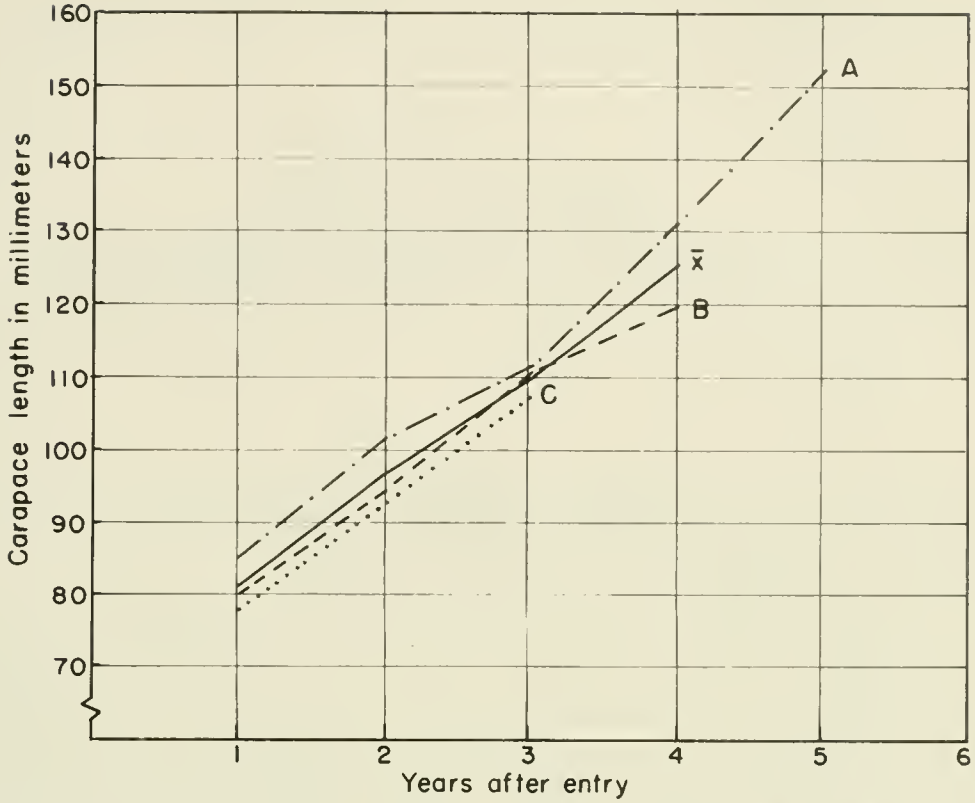

FIGURE 5.—Progressions of the mean values of size groups A, B, and C. $\bar{x}$ denotes the progression of the mean of the size group means.

of these means which shows a relatively constant increase of approximately 15 mm. per year.

Although modes other than those discussed were evident, only the more prominent ones in the smaller sizes were considered. This selection was guided by the suspicion that due to the lesser frequency of molting in the larger sizes, an overlapping of year classes occurred, and the modes or means of individual classes became unidentifiable. To alleviate the problem of attempting to define annual growth in the large adult male king crabs by following the progressions of distinctively weak or dominant modes, another method was developed, which involves the determination of growth in length per molt and the proportions molting.

GROWTH INCREMENT PER MOLT

Three hundred and ten tagged and recaptured crabs representing growth from one molt (appendix table 3) range in size from 98 to 169 mm. before molting. The carapace length at release and the observed growth increments for these crabs are shown in figure 6.

The straight line shown in figure 6, fitted by the method of least squares, represents the regression of growth increment on size for the size range of our data. It is recognized that a second degree polynomial ($\hat{Y}=-62.989+1.1410X-0.0041X^2$) better fits the data, significantly reducing the mean square from 8.994 to 8.233. However, growth curves based on linear and curvilinear regressions were compared and it was found that the maximum difference at any one point between the curves did not exceed 2 mm. Since the use of a straight line regression simplifies subsequent discussions, and results are not appreciably affected, we have considered the growth increment for one molt as being represented by the straight line regression in figure 6. This line is expressed by the equation $\hat{Y}=13.14+0.018X$. The mean expected growth increment, $\hat{Y}$, varies from 15.1 mm. for a carapace length of 110 mm. to 16.0 mm. for carapace length 160 mm., a difference of only 0.9 mm. Thus the growth increment of crabs of these

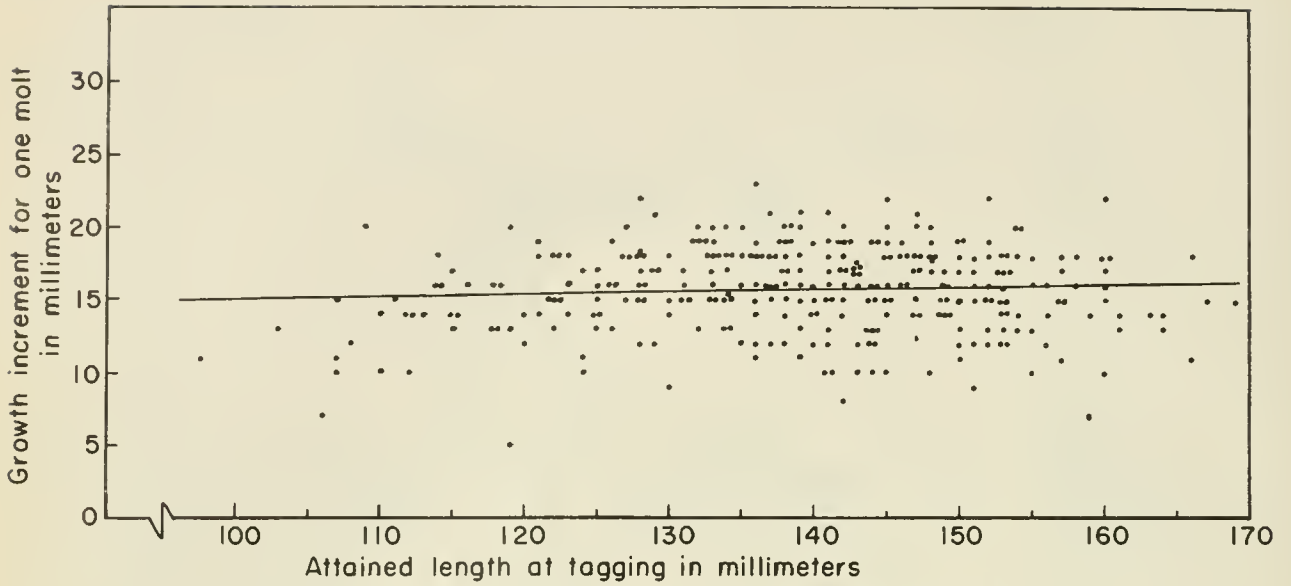

FIGURE 6.—Carapace length increment for one molt of 310 tagged crabs. The line represents the linear regression of growth increment on size as determined by the method of least squares.

sizes is essentially constant and for the purpose of this discussion we regard the growth increment per molt as being 16 mm. for all male crabs 110 mm. in carapace length and larger. Extrapolation of the regression line beyond 170 mm. may introduce error, but the results are not appreciably affected as only a small proportion of the crabs of these larger sizes molt.

AVERAGE ANNUAL GROWTH INCREMENT OF THE POPULATION

If all adult male crabs molted once annually, their growth would be described as an accumulation at the rate of 16 mm. per year. However, the small adults molt annually, but as they increase in size, molting occurs less frequently. Since we do not yet know the molting frequency of individual crabs, we cannot describe their growth rate. We can, however, determine the average annual growth of the population by adjusting the growth increase determined from tagged individuals by the proportions of molting crabs observed.

The numbers of non-molters (old-shell crabs) and molters (new-shell crabs) by size, observed in samples for the years 1956 through 1959, are shown in figure 7. Shell condition was not recorded in 1955.

Since all sizes of adult male crabs greater than 110 mm. in carapace length were shown to increase by approximately 16 mm. per molt, the new-shell distribution for each year was shifted 16 mm. to the left. This has the effect of returning the new-shells to their size prior to molting. We then smoothed both distributions by a moving average of 7 mm. and calculated the proportion of new-shell to old-shell crabs for each millimeter size class. The result of the transformation, using the 1958 data as an example, is shown in figure 8. By multiplying the proportions molting by 16 mm., the average annual growth increment of crabs greater than 110 mm. was calculated for each year's data and shown in figure 9.

AVERAGE GROWTH RATES

In any growth study it is highly desirable to define growth in terms such as the growth of individuals or of an age class. Until permanent records of growth are found in crabs, or tagged individuals are returned after prolonged periods of freedom, it is unlikely that the growth rate of individuals can be described. It appears possible, however, to estimate the average growth rate of a year class.

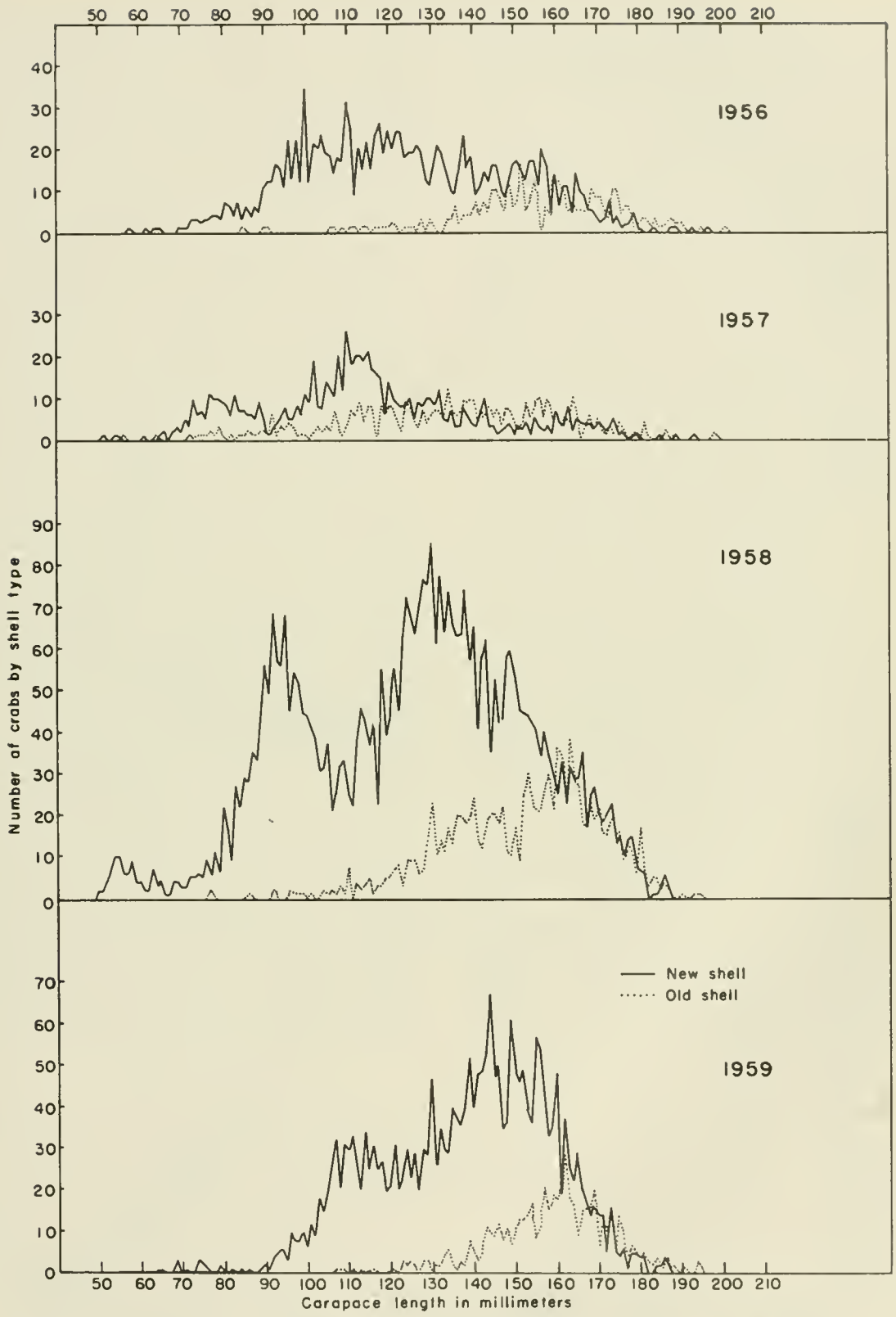

FIGURE 7.—Size-frequency distribution by shell condition for the years 1956 through 1959.

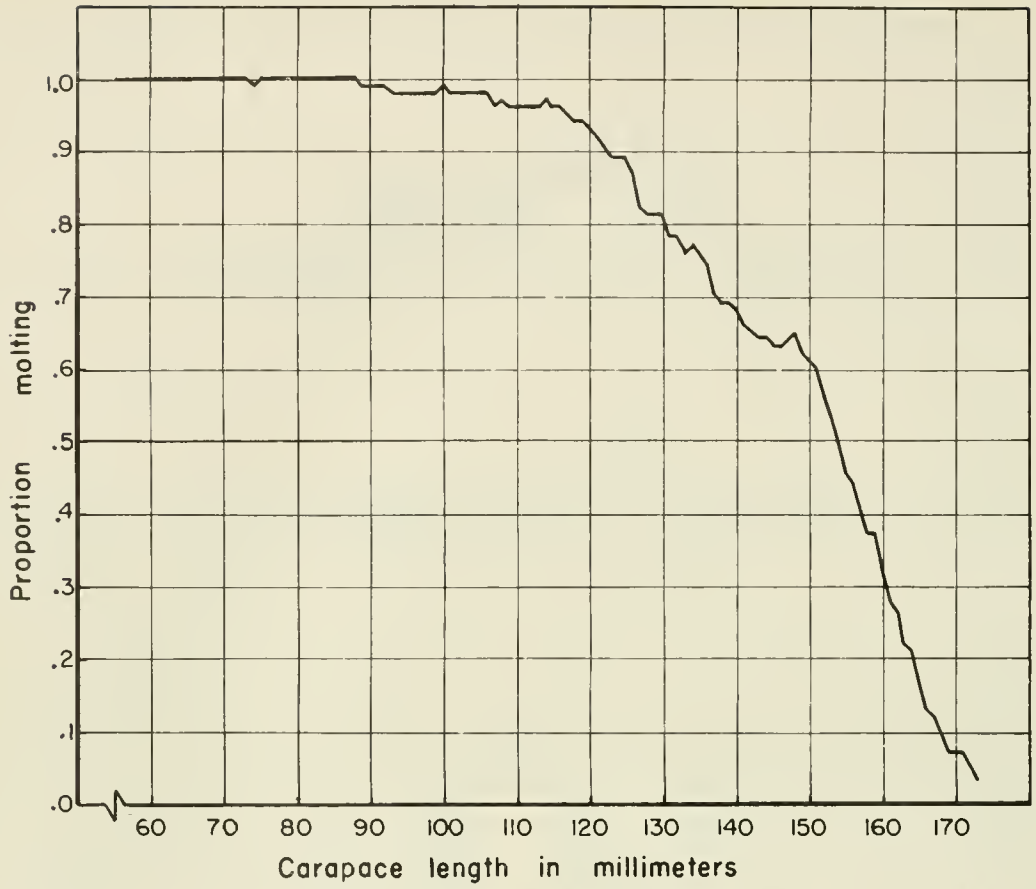

FIGURE 8.—Proportion of crabs molting, by size, as calculated from the 1958 sampling data.

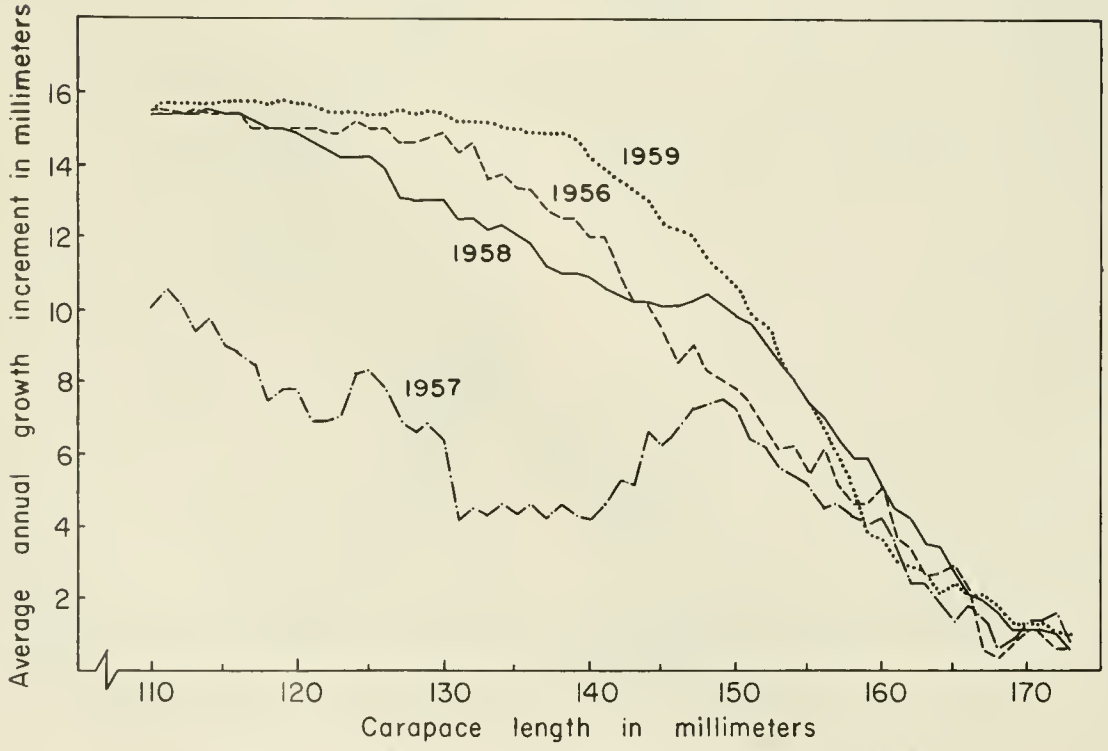

FIGURE 9.—Average annual growth increments for the years 1956–59.

The simplest method of estimating the average growth rate would appear to be a stepwise accumulation of the average annual growth increments. For example, using the 1958 data (fig. 9) and assuming that the growth increments represent growth potential in terms of length, crabs 110 mm. in length at some single age N would, on the average, increase in size by 15.4 mm., resulting at age $N+1$ in an average size of 125.4 mm. The average annual increment for 125.4 mm. crabs can then be added to determine the size at age $N+2$, etc. It can be seen that the average annual increment is the average amount of growth for all crabs of a size, and that the proportions used are made up of crabs that have, and those that have not, molted. The resulting relation of size with time by this accumulating process is, therefore, in terms of average size against average age.

To avoid the use of double averages, a method was developed to express the growth rate in terms of average size at a particular age. The method utilizes a model which we believe represents the growth of the eastern Bering Sea king crab stock, and depicts the advancement of a size group through 6 years.

We will examine a hypothetical group of 10,000 male crabs under the assumption that the attained sizes of several year classes in one year are representative of the growth of one year class from year to year. Basic inferences derived earlier in the report from tagging and from the sampling data for 1958 are utilized in a hypothetical model. These are: (1) when male king crabs 110 mm. and larger molt, the carapace length increases by 16 mm., and (2) the proportion molting by 16 mm. intervals (fig. 8) are: at 110 mm. carapace length, the proportion molting, P is 0.96; at 126 mm. $P=0.87$; at 142 mm. $P=0.65$; at 158 mm. $P=0.37$; and at 174 mm. $P=0.03$. Since there were no crabs larger than 195 mm. taken in 1958, we assume P at 190 mm. to be 0.02, allowing for a slight decrease in molting frequency.

The smallest size considered in the model is 110 mm., a size generally common to the progressions of modes described previously. Since most, if not all, crabs less than 110 mm. molt at least annually, and the modes in size frequency distributions of these sizes are quite definite, we assume that 110 mm. crabs in the model are all of one age class at N years of age. The sizes, numbers, and average size present in each of the successive years from age N to age $N+5$ are calculated and shown in table 3. At the end of the first year, since 96 percent of the 110-mm. crabs molt and 4 percent do not molt, the age group has been segregated into two size classes with an average length of 125.4 mm. The following year the crabs are of age $N+1$, and the 110-mm. crabs ($N=400$) and the 126 mm. crabs ($N=9,600$) are calculated to be distributed in varying numbers in three size classes consisting of 16 crabs remaining at 110 mm., 1,632 crabs at 126 mm., and the remaining 8,352 advancing to 142 mm. In this manner, at the end of the year of age $N+5$, five size classes are represented, the average length of the year class being 167.8 mm.

The 1956, 1957, and 1959 data are treated in the same manner, and the average lengths for each age for all years are tabulated in table 4. The growth curves based on the average sizes for each age are shown in figure 10. Both the table and the figure include an extension below 110 mm. to ages $N-1$ and $N-2$. The extension is the mean of the means of the progression of modes in the size frequency distribution discussed earlier.

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TABLE 3.—*A model representing the advancement of one size group of crabs following the growth trend as observed from the 1958 sampling data*

[Explanation of symbols: N, age in years; P, proportion molting; q, old shell]

Beginning of year					End of year							
Age in years N	Number of crabs	Carapace length in mm.	Proportion molting P	(1–P) q	Number of crabs by carapace length (mm.) and shell condition							Average size in mm.
					110	126	142	158	174	190	206	
N	10,000	110	0.96	0.04	[1] 400	9,600						
Total					400	9,600						125.4
$N+1$	400	110	.96	.04	[1] 16	384						
	9,600	126	.87	.13		[1] 1,248	8,352					
Total					16	1,632	8,352					139.3
$N+2$	16	110	.96	.04	[1] 1	15						
	384	126	.87	.13		[1] 50	334					
	1,248	126	.87	.13		[1] 162	1,086					
	8,352	142	.65	.35			[1] 2,923	5,429				
Total					1	227	4,343	5,429				150.3
$N+3$	1	110	.96	.04		1						
	15	126	.87	.13		[1] 2	13					
	50	126	.87	.13		[1] 6	44					
	162	126	.87	.13		[1] 21	141					
	334	142	.65	.35			[1] 117	217				
	1,086	142	.65	.35			[1] 380	706				
	2,923	142	.65	.35			[1] 1,023	1,900				
	5,429	158	.37	.63				[1] 3,420	2,009			
Total					0	30	1,718	6,243	2,009			158.4
$N+4$	1	126	.87	.13			1					
	2	126	.87	.13			2					
	6	126	.87	.13		[1] 1	5					
	21	126	.87	.13		[1] 3	18					
	13	142	.65	.35			[1] 5	8				
	44	142	.65	.35			[1] 15	29				
	141	142	.65	.35			[1] 49	92				
	117	142	.65	.35			[1] 41	76				
	380	142	.65	.35			[1] 133	247				
	1,023	142	.65	.35			[1] 358	665				
	217	158	.37	.63				[1] 137	80			
	706	158	.37	.63				[1] 445	261			
	1,900	158	.37	.63				[1] 1,197	703			
	3,420	158	.37	.63				[1] 2,155	1,265			
	2,009	174	.03	.97					[1] 1,949	60		
Total					0	4	627	5,051	4,258	60		164.0
$N+5$	1	126	0.87	0.13			1					
	3	126	0.87	0.13			3					
	1	142	.65	.35				1				
	2	142	.65	.35			[1] 1	1				
	5	142	.65	.35			[1] 2	3				
	18	142	.65	.35			[1] 6	12				
	5	142	.65	.35			[1] 2	3				
	15	142	.65	.35			[1] 5	10				
	49	142	.65	.35			[1] 17	32				
	41	142	.65	.35			[1] 14	27				
	133	142	.65	.35			[1] 47	86				
	358	142	.65	.35			[1] 125	233				
	8	158	.37	.63				[1] 5	3			
	29	158	.37	.63				[1] 18	11			
	92	158	.37	.63				[1] 58	34			
	76	158	.37	.63				[1] 48	28			
	247	158	.37	.63				[1] 156	91			
	665	158	.37	.63				[1] 419	246			
	137	158	.37	.63				[1] 86	51			
	445	158	.37	.63				[1] 280	165			
	1,197	158	.37	.63				[1] 754	443			
	2,155	158	.37	.63				[1] 1,358	797			
	80	174	.03	.97					[1] 78	2		
	261	174	.03	.97					[1] 253	8		
	703	174	.03	.97					[1] 682	21		
	1,265	174	.03	.97					[1] 1,227	38		
	1,949	174	.03	.97					[1] 1,891	58		
	60	190	.02	.98						[1] 59	1	
Total					0	0	223	3,590	6,000	186	1	167.8

[1] Old shell.

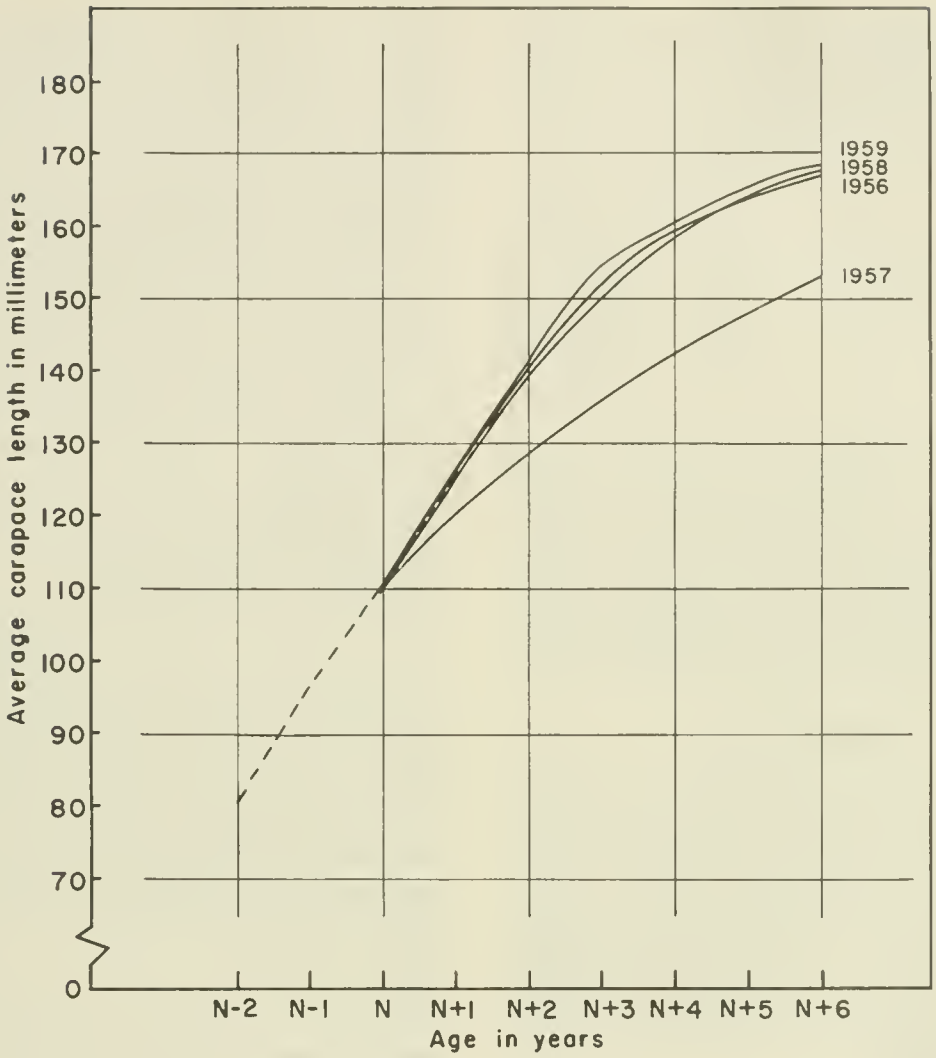

FIGURE 10.—Average growth curves of adult male king crabs for each of the years 1956 through 1959 as determined from population models (solid lines). The broken line extension represents the average progression of modes in the size frequency distributions. *N* represents an age in years at which crabs are 110 mm. in carapace length.

TABLE 4.—*Average size at each age of the southeastern Bering Sea population of adult male king crabs as determined from modal progression in size-frequency distribution and from growth per molt multiplied by the molting proportions in each size*

Age	Average sizes present by year			
	1956	1957	1958	1959
$N-2$	80.7	80.7	80.7	80.7
$N-1$	96.0	96.0	96.0	96.0
N	110.1	110.1	110.1	110.1
$N+1$	125.5	120.1	125.4	125.4
$N+2$	140.6	128.7	139.3	140.9
$N+3$	152.0	136.1	150.3	154.6
$N+4$	159.0	142.5	158.4	161.4
$N+5$	163.7	148.1	164.0	165.4
$N+6$	167.2	153.0	167.8	168.4

It would be unrealistic to extend the growth model beyond $N+6$, because very few crabs greater than 200 mm. in carapace length are taken in the eastern Bering Sea. In addition, from the curves presented, it appears that in most years the average length is approaching an asymptote, and any further increase in age will not greatly affect the average size of the year class.

DISCUSSION

The growth rates calculated from the 1956, 1958, and 1959 data show general agreement, but 1957 data suggests an appreciably lower rate. This is due primarily to the apparent lower proportion of molters in the 110- to 150-mm. carapace length range. In view of the discrepancy of the 1957 data, and because of the few years for which we have data, no attempt has been made to develop a single growth curve.

The model assumes that molting rate is a function of size. It might be questionable that crabs of any one size, which did not molt, will exhibit the same molting rate the following year. The molting proportion, P, used in the model are the proportions observed in the entire sample (population), and in the larger sizes undoubtedly includes several year classes with crabs of various shell conditions. The assumption that crabs of a common size, with varying time since the last molt, have equal molting rates is guided by the fact that the P's are averages of all molting rates that occur in the eastern Bering Sea; that is, the molting rates of new-shell and old-shell and, to a lesser degree, very-old-shell crabs make up P.

If molting rates of the various shell conditions differ widely, they must differ around P; that is, any large deviation of the molting rate of one shell type from P must be accompanied by a compensating deviation of one or both of the other. For example, if the molting rate of old-shell crabs is high, the molting rate of new-shell crabs would be low, and in any particular year of the age-class progression where old-shell crabs predominate, the average size would be greater than that indicated in the model. However, in the following year the increased number of new-shell crabs resulting from the high-molting rate of the old-shell crabs would be subject to the low molting rate of crabs having new shells. The result would be a lower average size of the year class for that year. The growth rate under such a condition would be step-like, and smoothing would result in a curve that would approximate that developed by considering P constant for size, as we have done.

Observed molting proportions may also be affected by other factors: (1) varying environmental conditions, (2) varying year class strength, (3) differential natural mortalities by shell conditions, and size. Our studies with respect to the above factors have not progressed sufficiently to measure their effect on molting proportions.

The model does not consider mortality. Although this may be unrealistic, mortality was not included since our measures of mortality rates are not yet definitive, and constant loss would not change the results.

There is no reason to expect appreciable differential natural mortality by size or age for the range of size and age being discussed here. It might be expected, however, that there would be a higher death rate of crabs that molt than those that do not. The effect of molting mortality is negated by the fact that molting proportions are based on numbers surviving; therefore, after the effect of molting mortality. Although there is some differential mortality due to fishing, since the fishery continually strives to catch the larger old-shell male crabs, this mortality is not evaluated in the model. The fishery operates concurrently with our sampling efforts, and at present there is no way to assess its effects. In addition, preliminary examination shows that the fishery, through 1959, takes a relatively small proportion of the king crab population as a whole.

For use in calculation of yield, it would be expedient to express our growth curves as mathe-

matical functions. At present, however, the complexity of interdependence of growth, mortality, and recruitment precludes the mathematical formulation of a growth parameter which is suitable for analytical purposes. Either elimination or determination of the interaction of mortality and recruitment on our data must be resolved first; for prediction of yield under varying conditions requires that each parameter be independent or in terms of coefficients which represent the magnitude of their integrated effect. Also, the growth rate presented represents the average growth of the population by lengths and would, for the purpose of calculating yields, be more meaningful if presented in terms of weights. The king crab's live weight is, however, not very significant, since meat-weight is subject to wide variation for any one size, while body-weight remains essentially constant. Therefore, it seems more appropriate to discuss growth by weights and resulting yield in a study of productivity.

It would be desirable to compare the growth curves developed in this paper with those of Marukawa (1933), Nakazawa (1912), and Wang (1937), presented earlier. The Marukawa and Wang growth curves are based on size intervals between modes and progression of modes in size-frequency distributions which would tend to reflect the growth of only molting crabs. Nakazawa bases his curve on growth increment per molt and frequency of molt which he assumes occurs at least once a year. Thus, his curve would also reflect primarily the growth of only molting crabs. The curves developed in our paper, on the other hand, are weighted by the proportion of each size that does not molt and for the larger sizes particularly will show a slower growth rate. Therefore, the curves developed by the authors cited and those described in this report are not directly comparable.

Considering the rate of growth concerning juvenile crabs, as shown by the data of the above investigations and our observations in Unalaska Bay, we speculate that an 80-mm. crab ($N-2$) in the eastern Bering Sea may be about 4 years old. We hesitate, however, to place a precise estimate of size and corresponding age on our N values until the present juvenile crab studies are further advanced.

SUMMARY

During the 6 years (1954–59) the U.S. Fish and Wildlife Service has carried on a study of the southeastern Bering Sea king crab *Paralithodes camtschatica*. One phase of the investigations has been to estimate the rate of growth of the adult male king crab.

Estimating the growth rate required the use of three factors: (1) group progression in size-frequency distribution; (2) growth increment per molt; and (3) the proportion of each size molting in any given year.

Observations of size group advancement through 5 years of size-frequency distribution samples afforded an estimate of the growth rate for the smaller adult crabs. Results show that a size group of crabs averaging 81 mm. in carapace length attains a length of 126 mm. after three years—an annual growth increment of 15 mm.

Tagged crabs measured at release and again at recovery provided data indicating that the growth per molt is approximately 16 mm. for all crabs more than 110 mm. in length. The proportion molting for each size was calculated from observations on shell condition reported during each year of the station-pattern sampling program. By combining growth per molt and the proportion molting, the average annual growth increment of crabs greater than 110-mm. carapace length is calculated. The resulting curves for each year of sampling exhibited a rapidly decreasing average annual growth increment as the crabs increase in size.

The growth rate of crabs, greater than 110 mm. in length, was estimated by employing a model which represents the progression of a year class through time for each of the years 1956–59.

The growth rates as estimated from size-group progression and the model method were combined. The resulting growth curves calculated from the 1956, 1958, and 1959 data were quite similar, and showed that on the average, male crabs 80 mm. in carapace length will attain a length of 168 mm. after 8 years of growth. Crabs growing at the rate depicted for 1957 would be 153 mm. in length at the end of an equal period. The reduced growth rate for 1957 was due primarily to the lower frequency of molting recorded in the 110 to 150 mm. sizes.

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APPENDIX

The following tables of data on the king crab are those on which the figures and calculations in the text are based.

APPENDIX TABLE 1.—*Size frequency distribution and size frequency by shell conditions of mate king crabs from sampling data taken in each of the years 1955–59*

Carapace length in mm.	1955 [1] total	1956			1957			1958			1959		
		Shell condition		Total	Shell condition		Total	Shell condition		Total	Shell condition		Total
		New	Old		New	Old		New	Old		New	Old	
50								2		2			
51					1		1	2		2			
52								4		4			
53								6		6			
54					1		1	10		10			
55					1		1	10		10			
56						1	1	6		6			
57								6		6			
58		1		1				9		9			
59								4		4			
60								4		4			
61					1		1	2		2			
62		1		1				2		2			
63								7		7			
64		1		1		1	1	3		3	1		1
65		1		1	1		1	4		4	1		1
66					2		2	1		1			
67								1		1			
68					2		2	4		4	1		1
69					3		3	4		4	3		3
70	1	1		1	2		2	3		3			
71		1		1	5		5	3		3	1		1
72		1		1	3	1	4	5		5			
73	1	3		3	10		10	5		5	1		1
74	2	3		3	6	1	7	6		6	3		3
75	3	2		2	7	1	[2] 9	5		5	2		2
76	5	3		3	5	1	6	9		9	1		1
77	7	3		3	11	2	13	6	2	8			
78	2	4		4	10	1	11	11		11			
79	4	4		4	8	3	11	7		7	2		2
80	6	3		3	9	1	10	22		22			
81	5	7		7	8		8	17		17			
82	5	6		6	6	1	7	9		9	1		1
83	5	4		4	11		11	27		27			
84	5	7		7	7	1	8	22		22	1		1
85	3	3	1	4	7	1	8	29		29			
86	10	6		6	6	2	8	28	1	29	1		1
87	6	4		4	6	1	7	35		35			
88	5	6		6	5	1	6	33		33			
89	3	5		5	9	2	11	44		44	1		1
90	3	10	1	11	4	2	6	56		56	2		2
91	8	12	1	13	1	1	2	49		49	1		1
92	3	12		12	3	6	9	68	2	70	4		4
93	7	16		[2] 17	4	1	5	57		57	5		5
94	4	15		15	6	3	9	56		56	6		6
95	3	11		[2] 12	8	2	10	68		68	3		3
96	7	22		22	5	4	9	45	2	47	10		10
97	9	13		13	5	3	8	54	1	55	8		8
98	4	22		22	8	1	9	51	1	52	8		8
99	5	12		12	6	1	7	45	1	46	10		10
100	7	34		34	11	1	12	44		44	7		7
101	4	12		12	9		9	42	1	43	12		12
102	5	21		21	19	2	21	38		38	9		9
103	6	20		20	8	3	11	31		31	18		18
104	3	23		23	7	2	9	31	2	33	15		15
105	3	19		19	14	3	17	37	1	38	21		21
106	4	18	1	19	12	2	14	21	2	23	27		27
107	3	14	1	15	15	7	22	26	1	27	32	1	33
108	5	18		[2] 19	20	3	23	32	3	35	21	1	22
109	3	17	1	18	12	1	13	33	1	34	31	1	[2] 33
110	4	31		31	26	4	30	25	7	32	30		30
111	2	24	1	25	18	7	25	22		22	33	1	34
112	6	9	1	10	20	6	26	35	4	39	26		26
113	10	20		[2] 21	20	9	29	46	2	48	20	1	21
114	8	15	1	16	19	4	23	43	3	46	34		34
115	5	21	1	22	21	8	29	37	5	42	25	1	26
116	6	15		15	17	8	25	42	1	43	31	1	32
117	5	23	1	24	16	1	17	23	3	26	25		25
118	9	26	1	[2] 28	15	8	23	55	3	58	27		27
119	3	19	1	20	6	7	13	39	5	44	20		20
120	5	24	1	[2] 26	14	8	22	43	5	[3] 49	21	1	22

[1] See footnotes at end of table.

APPENDIX TABLE 1.—*Size frequency distribution and size frequency by shell conditions of male king crabs from sampling data taken in each of the years 1955–59*—Continued

Carapace length in mm.	1955 [1] total	1956			1957			1958			1959		
		Shell condition		Total	Shell condition		Total	Shell condition		Total	Shell condition		Total
		New	Old		New	Old		New	Old		New	Old	
121	8	20	2	22	10	8	18	55	7	62	31	1	32
122	7	24	1	25	9	4	13	45	8	53	20		20
123	4	24		[2] 25	8	2	10	63	3	66	23	3	26
124	5	18	1	[2] 20	8	9	17	72	9	81	30	2	32
125	10	19	1	20	10	8	18	67	9	76	23	3	26
126	3	19	1	[2] 21	5	5	10	63	9	72	29	1	30
127	6	21		21	14	3	17	71	6	77	20	1	21
128	10	19	3	22	8	7	15	76	7	83	30	3	33
129	6	13		13	10	4	14	75	14	89	29	3	32
130	7	11	3	[2] 15	10	6	16	85	23	108	47		47
131	5	17	1	18	8	7	15	61	10	71	26	2	28
132	8	21		[2] 22	12	7	19	77	14	91	35	2	37
133	5	19		19	5	5	10	64	11	75	31	4	35
134	6	14	3	17	4	12	16	73	17	90	29	6	35
135	6	10	3	[2] 14	7	7	14	66	13	79	40	2	42
136	6	9	6	15	3	6	9	63	20	[2] 84	37	1	38
137	7	14	2	16	3	7	10	63	20	83	36	3	39
138	6	23	4	27	8	9	17	74	18	92	40	2	42
139	8	15	4	19	6	9	15	57	19	76	52	8	60
140	7	18	4	22	4	10	14	65	24	89	40	5	45
141	4	9	7	16	3	5	8	41	14	55	48	3	51
142	11	10	4	14	7	7	14	57	12	70	49	5	54
143	12	14	7	21	10	6	16	62	18	80	53	11	64
144	6	12	4	16	3	8	11	35	20	55	67	10	77
145	9	16	10	[2] 27	3	5	8	52	20	72	47	9	[2] 57
146	5	16	10	26	1	7	8	42	18	60	50	12	[2] 63
147	11	11	7	18	2	3	5	43	22	65	35	8	43
148	9	8	5	13	3	7	10	58	11	69	36	11	47
149	7	11	14	25	4	7	11	59	10	69	61	7	68
150	9	16	6	[2] 23	1	4	5	53	17	70	49	11	60
151	7	17	7	24	5	2	7	45	9	54	46	13	59
152	4	14	16	[2] 31	2	4	6	44	23	67	49	13	62
153	8	12	5	17	4	9	13	44	30	74	41	14	55
154	11	17	7	[2] 25	1	5	6	42	23	65	36	17	53
155	11	17	12	[2] 30	5	9	14	40	21	61	57	8	65
156	7	11	8	19	3	10	13	34	21	55	54	12	66
157	1	20		[2] 21	2	5	7	40	26	66	41	21	62
158	7	16	6	22	3	10	13	34	30	64	33	15	48
159	7	5	4	9	1	5	6	31	21	52	35	19	54
160	3	14	13	27	7	7	14	25	36	61	48	18	66
161	9	6	12	18	4	3	7	33	34	67	19	22	41
162	3	11	10	21	3	5	8	23	23	46	37	28	65
163	6	11	5	16	8	4	12	33	38	71	27	18	45
164	7	4	7	11	2	10	12	28	28	56	22	16	38
165	8	14	5	19	5	6	11	29	27	56	29	9	38
166	1	10	5	15	4		4	35	18	53	20	15	35
167	5	9	5	14	4	3	7	17	17	34	18	16	34
168	11	5	5	10	4	6	10	25	24	49	14	16	30
169	8	5	10	[2] 16	2	2	4	27	19	46	17	20	37
170	5	3	8	11	4	5	9	20	22	42	14	7	21
171	3	2	8	10	3	2	5	18	16	34	14	13	27
172	7	3	4	7	2	1	3	20	15	35	5	10	15
173	3	8	3	11	4	3	7	23	19	42	16	16	32
174	5	2	10	12	5	1	6	13	15	28	6	7	13
175	8	4	10	14	1	4	5	15	16	31	4	14	[2] 19
176	6	1	4	5	2	3	5	10	9	19	6	9	15
177	6	2	6	8	1		1	14	13	27	1	4	5
178	4	2	6	8				15	10	25	5	7	12
179	5	5	1	6	1	2	3	7	6	13	5	5	10
180	6	1	2	[2] 4	2		2	6	17	23	4	4	8
181	1		3	3		4	4	6	6	12	4	5	9
182			3			1	1		3	3		3	3
183	2		1	1				1	5	6		2	2
184	1	1	3	4				1	5	6	2	4	6
185	2		1	1	1	1	1	4	2	6	1	1	2
186	3		1	1		2	2	3	6	9	4	3	7
187	2		2	2				1	2	3	1	1	2
188		1	3	4		1	1					2	2
189	1	1	2	3	1	1	2						
190	1		2	2					1	1		2	2
191			1	1								1	1
192													
193		1		1	1		1		1	1			
194									1	1		3	3
195			1	1									
196													
197		1		1									
198						1	1						
199													
201			1	1									
Total	645	1,375	355	1,750	808	470	1,279	4,354	1,140	[3] 5,496	2,440	580	3,024

[1] Shell condition not recorded in 1955.
[2] One crab of unknown shell conditions.
[3] Eight additional crabs under 50 millimeters.

APPENDIX TABLE 2.—*One hundred twenty-eight within-year tag recoveries*

Year released	Release		Recovery		Deviation from release measurement at recovery
	Carapace length	Carapace width	Carapace length	Carapace width	Carapace length
	mm.	*mm.*	*mm.*	*mm.*	*mm.*
1955	150	170	146	173	−4
1955	191	229	188	229	−3
1955	168	202	170	203	2
1955	145	160	142	161	−3
1955	168	200	157	182	−11
1955	145	170	143	170	−2
1955	128	146	128	143	0
1955	137	155	135	156	−2
1955	177	220	176	220	−1
1955	167	200	167	201	0
1955	118	131	118	132	0
1955	171	203	170	202	−1
1955	155	178	155	179	0
1955	157	186	156	188	−1
1955	160	187	160	187	0
1955	147	173	148	174	1
1955	156	184	155	183	−1
1955	175	208	173	209	−2
1955	163	199	163	200	0
1955	178	211	177	210	−1
1955	167	202	165	Unknown	−2
1955	173	204	173	206	0
1955	169	196	169	198	0
1955	138	160	138	158	0
1955	172	201	171	202	−1
1956	128	147	127	146	−1
1956	149	177	149	173	0
1956	120	139	119	139	−1
1956	149	175	148	175	−1
1956	161	188	160	186	−1
1956	142	169	143	169	1
1956	157	186	157	184	0
1956	147	171	147	170	0
1956	154	183	154	184	0
1956	175	210	176	208	1
1956	150	182	150	180	0
1956	138	161	139	160	1
1956	157	183	156	182	−1
1956	131	149	131	147	0
1956	172	204	171	204	−1
1956	138	163	137	162	−1
1956	159	183	156	185	−3
1956	160	188	157	192	−3
1956	155	177	154	178	−1
1956	166	189	166	190	0
1956	148	177	147	176	−1
1956	146	165	146	167	0
1956	166	198	167	196	1
1956	147	176	146	174	−1
1956	150	176	151	177	1
1956	147	180	147	181	0
1956	151	176	152	177	1
1956	153	181	153	182	0
1956	151	180	152	182	1
1956	160	189	159	190	−1
1956	145	168	145	170	0
1956	162	192	162	192	0
1956	162	184	160	180	−2
1956	150	178	150	175	0
1956	155	183	154	179	−1
1956	155	182	152	182	−3
1956	155	184	155	186	0
1958 [1]	132	155	132	156	0
1958	95	108	95	108	0
1958	162	188	161	193	−1

APPENDIX TABLE 2.—*One hundred twenty-eight within-year tag recoveries*—Continued

Year released	Release		Recovery		Deviation from release measurement at recovery
	Carapace length	Carapace width	Carapace length	Carapace width	Carapace length
	mm.	*mm.*	*mm.*	*mm.*	*mm.*
1958	157	191	156	192	−1
1958	149	171	148	169	−1
1958	168	203	168	201	0
1958	172	204	171	207	−1
1958	158	191	159	193	1
1958	161	197	163	196	2
1958	164	185	162	190	−2
1958	144	170	143	173	−1
1958	164	193	163	198	−1
1958	157	185	157	189	0
1958	186	213	185	220	−1
1958	161	187	161	190	0
1958	158	184	157	187	−1
1958	170	206	170	210	0
1958	184	217	183	226	−1
1958	181	210	181	213	0
1958	176	209	176	210	0
1958	175	208	175	209	0
1958	173	205	173	212	0
1958	144	166	143	168	−1
1958	165	200	165	202	0
1958	172	202	170	205	−2
1958	158	183	158	185	0
1958	164	196	164	197	0
1958	180	208	179	213	−1
1958	140	168	140	171	0
1958	160	183	158	188	−2
1958	152	173	151	175	−1
1958	162	196	161	195	−1
1958	137	163	138	163	1
1958	175	202	175	212	0
1958	166	193	167	196	1
1958	164	193	163	196	−1
1959	175	202	175	208	0
1959	143	167	142	170	−1
1959	166	195	165	196	−1
1959	152	182	151	185	−1
1959	175	208	173	214	−2
1959	162	186	162	191	0
1959	145	167	145	171	0
1959	171	203	170	207	−1
1959	167	197	167	199	0
1959	144	164	143	164	−1
1959	151	171	150	174	−1
1959	163	192	162	197	−1
1959	162	192	161	194	−1
1959	147	174	146	178	−1
1959	157	179	156	182	−1
1959	171	202	171	206	0
1959	164	194	163	199	−1
1959	162	188	162	191	0
1959	166	193	167	195	1
1959	167	190	166	196	−1
1959	153	176	153	177	0
1959	148	169	147	173	−1
1959	194	223	193	226	−1
1959	171	202	169	205	−2
1959	167	200	166	202	−1
1959	161	192	160	193	−1
1959	154	182	154	182	0
1959	148	172	149	175	1
1959	168	198	167	201	−1
1959	168	194	162	191	−6

[1] Carapace measurements of the 1957 within-year recoveries were not recorded.

APPENDIX TABLE 3.—*Spaghetti-type tag recoveries showing growth*

Release data				Recovery data				Growth increment	
Year	Carapace length	Carapace width	Shell condition	Year	Carapace length	Carapace width	Shell condition	Carapace length	Carapace width
	mm.	*mm.*			*mm.*	*mm.*		*mm.*	*mm.*
1955	159	187	Unknown	1956	166	192	Unknown	7	5
1955	148	173	do	1956	158	184	New	10	11
1955	131	144	do	1956	146	164	do	15	20
1955	147	169	do	1956	165	195	do	18	26
1955	109	124	do	1956	129	150	do	20	26
1955	136	156	New	1957	151	179	Old	15	23
1955	119	130	do	1957	139	156	do	20	26
1955	135	155	do	1957	149	176	do	14	25
1955	135	153	do	1957	153	176	do	18	23
1955	149	173	do	1957	166	201	do	17	28
1955	135	156	do	1957	153	181	do	18	25
1955	149	174	do	1957	163	195	do	14	21
1955	160	193	do	1957	176	217	do	16	24
1955	137	153	do	1957	153	174	do	16	21
1955	141	160	do	1957	151	179	New	10	19
1955	160	185	do	1957	170	210	Old	10	25
1955	148	170	do	1957	166	196	do	18	26
1955	120	133	do	1957	134	153	do	14	20
1955	141	160	do	1957	159	184	do	18	24
1955	133	158	do	1957	149	186	do	16	28
1955	153	173	do	1957	167	195	do	14	22
1955	134	149	do	1957	154	176	do	20	27
1955	143	169	do	1957	159	190	do	16	21
1955	138	159	do	1957	153	180	do	15	21
1955	128	149	do	1957	146	175	do	18	26
1955	126	144	do	1957	142	170	do	16	26
1955	127	143	do	1957	145	166	do	18	23
1955	141	152	do	1957	160	187	do	19	25
1955	144	161	Unknown	1958	157	180	do	13	19
1955	149	178	Old	1958	163	199	do	14	22
1955	152	178	Unknown	1958	164	194	do	12	16
1955	146	164	do	1958	164	191	do	18	27
1955	117	135	do	1958	147	174	New	30	[1] 39
1955	122	143	do	1958	151	181	Old	29	[1] 38
1955	142	163	do	1958	161	192	do	19	29
1955	138	157	do	1958	155	183	do	17	26
1955	155	176	do	1958	168	194	do	13	18
1955	139	165	do	1958	150	184	do	11	19
1955	142	161	do	1958	159	190	do	17	29
1955	149	179	do	1958	163	200	do	14	21
1955	146	171	do	1958	162	195	Very old	16	24
1955	134	158	do	1958	147	178	Old	13	20
1955	134	144	do	1958	171	196	New	37	[1] 52
1955	159	176	New	1958	173	202	Old	14	26
1955	143	161	Unknown	1959	162	192	Very old	19	31
1955	128	145	do	1959	163	195	Old	35	[1] 50
1955	144	166	do	1959	176	211	do	32	[1] 45
1955	125	139	do	1959	154	186	do	29	[1] 47
1955	123	138	do	1959	157	186	do	34	[1] 48
1955	111	129	do	1959	148	180	do	37	[1] 51
1955	161	186	do	1959	175	209	do	14	23
1955	153	175	do	1959	169	198	Very old	16	23
1955	136	152	do	1959	147	174	Old	11	22
1955	125	141	do	1959	153	181	do	28	40
1955	143	171	do	1959	160	197	Very old	17	26
1955	164	191	do	1959	177	211	do	13	20
1956	155	180	Old	1957	171	203	New	16	23
1956	145	170	New	1957	161	196	do	16	26
1956	122	138	do	1958	135	156	Old	13	18
1956	125	146	do	do	142	169	do	17	23
1956	150	175	Old	do	161	189	do	11	14
1956	130	153	do	do	139	164	do	9	11
1956	139	155	do	do	156	175	do	17	20
1956	153	174	do	do	170	193	do	17	19
1956	152	183	do	do	167	207	do	15	24
1956	148	177	do	do	166	202	do	18	25
1956	163	196	do	do	177	215	do	14	19
1956	147	176	do	do	161	194	do	14	18
1956	151	174	do	do	160	187	do	9	13
1956	149	175	do	do	164	189	do	15	14
1956	138	161	New	do	150	180	do	12	19
1956	132	151	do	do	151	177	do	19	26
1956	129	142	do	do	141	159	do	12	17
1956	125	147	do	do	139	167	do	14	20
1956	140	164	Old	do	155	183	do	15	19
1956	148	172	do	do	168	202	do	20	30
1956	164	195	New	do	178	217	do	14	22
1956	141	164	Old	do	154	186	do	13	22
1956	149	174	do	do	165	201	do	16	25
1956	137	155	do	do	152	178	do	15	23
1956	149	177	New	do	164	199	do	15	22
1956	122	139	do	do	137	158	do	15	19
1956	130	147	do	do	145	168	do	15	21
1956	148	176	Old	do	165	194	do	17	18

APPENDIX TABLE 3.—*Spaghetti-type tag recoveries, showing growth*—Continued

Release data				Recovery data				Growth increment	
Year	Carapace length	Carapace width	Shell condition	Year	Carapace length	Carapace width	Shell condition	Carapace length	Carapace width
	mm.	*mm.*			*mm.*	*mm.*		*mm.*	*mm.*
1956	151	172	Old	do	163	190	Old	12	18
1956	124	141	do	do	134	157	do	10	13
1956	142	161	New	do	161	186	do	19	25
1956	118	137	do	1959	134	157	do	16	20
1956	145	164	do	1959	163	189	do	18	25
1956	143	167	do	1959	160	194	do	17	27
1956	118	131	do	1959	154	181	Very old	36	[1] 50
1956	155	181	do	1959	173	209	Old	18	28
1956	148	170	do	1959	167	192	do	19	22
1956	152	173	do	1959	170	197	do	18	24
1956	150	178	Very old	1959	162	193	do	12	15
1956	107	119	New	1959	136	156	New	29	[1] 37
1956	156	185	Old	1959	168	202	Very old	12	17
1956	166	196	do	1959	177	210	Old	11	14
1956	161	188	do	1959	174	204	Very old	13	16
1956	147	174	do	1959	161	196	do	14	22
1956	152	176	New	1959	174	205	Old	22	29
1956	141	166	do	1959	156	187	do	15	21
1956	157	181	do	1959	175	204	Very old	18	23
1956	144	164	do	1959	163	195	Old	19	31
1956	143	168	do	1959	160	186	do	17	18
1956	142	167	do	1959	150	181	do	8	14
1956	148	179	do	1959	166	208	do	18	29
1956	145	166	do	1959	164	193	do	19	27
1956	156	181	do	1959	170	199	do	14	18
1956	128	153	do	1959	146	177	do	18	24
1956	157	187	do	1959	172	203	do	15	16
1956	169	193	do	1959	178	220	do	18	27
1956	131	156	do	1959	148	182	do	17	26
1956	128	147	do	1959	150	176	do	22	29
1956	129	151	do	1959	150	181	do	21	30
1956	147	169	do	1959	168	196	do	21	27
1956	131	146	do	1959	146	165	do	15	19
1956	136	159	do	1959	152	182	do	16	23
1956	133	156	do	1959	153	187	do	20	31
1956	132	157	do	1959	152	187	do	20	30
1956	146	176	do	1959	153	185	do	7	9
1956	135	157	do	1959	155	181	do	20	24
1956	147	178	Old	1959	165	205	Very old	18	27
1956	138	164	New	1959	154	186	do	16	22
1956	133	155	do	1959	151	177	Old	18	22
1956	139	156	do	1959	154	175	do	15	21
1956	145	160	do	1959	167	192	do	22	32
1956	146	173	do	1959	166	202	do	20	29
1956	160	182	do	1959	182	212	do	22	30
1956	137	160	do	1959	153	183	do	16	23
1956	136	154	New	1959	159	180	Old	23	26
1956	154	176	do	1959	174	204	do	20	28
1956	154	179	do	1959	166	199	do	12	20
1956	153	178	do	1959	168	201	do	15	23
1956	153	173	do	1959	171	197	do	18	24
1956	141	169	Old	1959	151	183	Very old	10	14
1956	145	168	do	1959	155	181	Old	10	13
1956	140	160	New	1959	154	180	do	14	20
1956	143	161	Old	1959	153	176	Very old	10	15
1956	147	166	New	1959	167	195	Old	20	29
1956	146	173	do	1959	164	200	do	18	27
1956	154	179	do	1959	174	207	do	20	28
1956	134	156	do	1959	152	178	do	18	22
1957	128	145	Old	1958	140	163	New	12	18
1957	133	147	New	1958	148	171	do	15	24
1957	107	121	do	1958	117	137	do	10	16
1957	113	127	do	1958	127	151	do	14	24
1957	125	144	do	1958	139	162	do	14	18
1957	112	129	do	1958	126	151	do	14	22
1957	106	119	do	1958	113	126	do	7	7
1957	110	125	do	1958	120	140	do	10	15
1957	119	133	Old	1958	124	144	do	5	11
1957	114	127	New	1958	130	150	do	16	20
1957	128	147	do	1958	144	170	do	16	23
1957	126	142	do	1958	145	168	do	19	24
1957	107	117	do	1958	122	141	do	15	24
1957	118	134	do	1958	134	156	do	16	22
1957	116	134	do	1958	132	154	do	16	20
1957	112	123	do	1958	126	141	do	14	18
1957	121	136	Old	1959	135	155	Old	14	19
1957	127	142	do	1959	147	170	do	20	28
1957	153	182	Very old	1959	167	205	do	14	23
1957	122	142	Old	1959	137	167	do	15	25
1957	153	178	do	1959	166	200	Very old	13	22
1957	115	128	New	1959	128	150	New	13	22
1957	142	168	Old	1959	158	190	Very old	16	22
1957	140	156	do	1959	156	178	do	16	22
1957	138	159	do	1959	157	186	do	19	27

See footnote at end of table.

APPENDIX TABLE 3.—*Spaghetti-type tag recoveries, showing growth*—Continued

Release data				Recovery data				Growth increment	
Year	Carapace length	Carapace width	Shell condition	Year	Carapace length	Carapace width	Shell condition	Carapace length	Carapace width
	mm.	*mm.*			*mm.*	*mm.*		*mm.*	*mm.*
1957	123	141	Old	1959	139	166	Old	16	25
1957	157	190	do	1959	174	215	do	17	25
1957	127	141	do	1959	145	164	do	18	23
1957	135	152	do	1959	147	170	do	12	18
1957	147	172	do	1959	164	196	do	17	24
1957	136	160	New	1959	148	175	do	12	15
1957	151	176	Very old	1959	168	201	Very old	17	25
1957	128	145	New	1959	145	167	Old	17	22
1957	128	148	Old	1959	143	171	do	15	23
1957	134	147	do	1959	149	170	do	15	23
1957	107	118	New	1959	118	134	do	11	16
1957	142	157	do	1959	160	186	Very old	18	29
1957	141	160	Very old	1959	158	184	Old	17	24
1957	138	160	Old	1959	157	188	do	19	28
1957	145	163	Very old	1959	163	191	Very old	18	28
1957	137	160	New	1959	153	182	do	16	22
1957	137	154	Very old	1959	155	182	Old	18	28
1957	158	185	Old	1959	174	211	Very old	16	26
1957	145	169	do	1959	161	193	Old	16	24
1957	103	115	do	1959	116	136	do	13	21
1957	138	154	Very old	1959	156	182	do	18	28
1957	160	184	do	1959	177	208	Very old	17	24
1957	141	160	do	1959	157	183	Old	16	23
1957	122	132	Old	1959	161	181	New	39	[1] 49
1957	125	140	do	1959	140	162	Old	15	22
1957	139	155	Very old	1959	160	188	do	21	33
1957	139	161	Old	1959	155	[2]	do	16	[2]
1957	130	145	do	1959	148	169	do	18	24
1957	146	167	do	1959	165	195	do	19	28
1957	137	156	do	1959	158	181	do	21	25
1957	134	151	do	1959	149	172	do	15	21
1957	109	122	New	1959	139	162	New	30	[1] 40
1957	132	153	Old	1959	151	179	Old	19	26
1957	122	137	do	1959	140	159	do	18	22
1957	131	157	do	1959	147	181	do	16	24
1957	144	167	do	1959	159	188	do	15	21
1957	98	109	New	1959	109	121	do	11	12
1957	142	168	Old	1959	162	192	do	20	24
1957	132	155	New	1959	151	184	do	19	29
1957	134	155	do	1959	149	179	do	15	24
1957	153	174	Old	1959	170	201	do	17	27
1957	133	153	New	1959	148	176	do	15	23
1957	136	157	do	1959	152	183	do	16	26
1957	142	156	Old	1959	159	181	do	17	25
1957	140	167	do	1959	159	193	do	19	26
1957	143	167	do	1959	160	192	do	17	25
1957	158	186	do	1959	176	213	do	18	27
1957	166	185	do	1959	184	225	do	18	40
1957	128	144	do	1959	144	167	do	16	23
1957	126	145	New	1959	142	168	do	16	23
1957	154	181	Old	1959	168	203	do	14	22
1957	142	167	New	1959	156	187	do	14	20
1957	153	180	Old	1959	171	207	do	18	27
1957	137	149	do	1959	149	171	do	12	22
1957	122	142	New	1959	137	165	New	15	23
1957	152	175	Old	1959	171	204	Old	19	29
1957	154	184	do	1959	167	206	do	13	22
1957	134	156	do	1959	147	177	do	13	21
1957	132	150	New	1959	145	169	do	13	19
1957	124	148	do	1959	135	164	do	11	16
1957	121	138	do	1959	140	163	do	19	25
1957	124	140	Old	1959	141	165	do	17	25
1957	151	172	do	1959	169	201	do	18	29
1957	121	139	New	1959	139	163	do	18	24
1957	127	141	do	1959	142	163	do	15	21
1957	141	157	Old	1959	162	188	do	21	31
1957	128	146	New	1959	143	165	do	15	19
1957	149	178	Old	1959	165	201	do	16	23
1957	167	187	Very old	1959	182	219	do	15	32
1957	138	156	Old	1959	158	186	do	20	30
1957	144	168	do	1959	154	182	do	10	14
1957	157	186	do	1959	172	209	do	15	23
1957	115	131	New	1959	149	176	New	34	[1] 45
1957	160	190	Very old	1959	175	216	Old	15	26
1957	155	183	Old	1959	165	201	do	10	18
1957	111	126	New	1959	126	147	do	15	21
1957	115	130	Old	1959	132	152	do	17	22
1957	140	164	do	1959	154	181	do	14	17
1957	115	128	New	1959	129	148	do	14	20
1957	156	182	do	1959	172	208	do	16	26
1957	143	164	Old	1959	155	182	do	12	18

APPENDIX TABLE 3.—*Spaghetti-type tag recoveries, showing growth*—Continued

Release data				Recovery data				Growth increment	
Year	Carapace length	Carapace width	Shell condition	Year	Carapace length	Carapace width	Shell condition	Carapace length	Carapace width
	mm.	*mm.*			*mm.*	*mm.*		*mm.*	*mm.*
1957	125	150	Old	1959	138	168	New	13	18
1957	110	127	New	1959	124	147	do	14	20
1957	118	140	do	1959	131	162	do	13	22
1957	145	163	Old	1959	160	182	do	15	19
1957	114	131	do	1959	132	153	do	18	22
1957	144	176	do	1959	159	196	do	15	20
1957	154	177	Very old	1959	172	205	do	18	28
1957	139	162	New	1959	159	193	do	20	31
1957	139	162	Old	1959	157	188	do	18	26
1957	152	179	Very old	1959	168	206	do	16	27
1957	108	128	New	1959	120	144	do	12	16
1957	126	142	Old	1959	139	161	do	13	19
1957	136	157	New	1959	155	185	do	19	28
1957	152	177	Very old	1959	167	200	do	15	23
1957	138	159	New	1959	157	188	do	19	29
1957	128	153	Old	1959	146	177	do	18	24
1957	144	168	Very old	1959	156	186	Old	12	18
1957	151	172	Old	1959	166	194	do	15	22
1957	123	142	New	1959	141	171	do	18	29
1957	120	137	do	1959	132	154	do	12	17
1957	115	127	do	1959	129	147	do	14	20
1957	129	149	Old	1959	146	175	do	17	26
1957	125	147	New	1959	141	168	do	16	21
1957	119	132	do	1959	132	149	do	13	17
1957	138	159	Very old	1959	155	185	do	17	26
1957	112	126	New	1959	122	140	New	10	14
1957	118	133	do	1959	131	152	Old	13	19
1957	134	152	Very old	1959	151	178	do	17	26
1957	122	135	New	1959	140	162	do	18	27
1957	135	154	do	1959	151	177	do	16	23
1957	133	151	Very old	1959	150	178	do	17	27
1957	133	149	do	1959	151	177	do	18	28
1957	104	113	Old	1959	131	149	New	27	[1] 36
1957	144	170	Very old	1959	157	192	Old	13	22
1957	150	174	do	1959	165	198	Very old	15	24
1957	138	154	do	1959	152	178	Old	14	24
1957	130	151	Old	1959	144	168	do	14	17
1957	133	159	Very old	1959	151	186	do	18	27
1957	137	150	do	1959	153	173	do	16	23
1957	134	158	do	1959	152	183	do	18	25
1957	150	177	do	1959	167	198	do	17	21
1957	114	128	Old	1959	130	148	do	16	20
1957	144	164	Very old	1959	161	190	do	17	26
1957	160	187	Old	1959	178	215	do	18	28
1957	140	163	do	1959	152	185	do	12	22
1957	139	166	Very old	1959	152	187	do	13	21
1957	152	171	Old	1959	165	193	do	13	22
1957	141	165	do	1959	156	188	do	15	23
1957	157	176	Very old	1959	168	198	do	11	22
1957	151	170	do	1959	167	195	do	16	25
1957	145	170	do	1959	160	193	Very old	15	23
1957	136	158	Old	1959	154	187	Old	18	29
1957	146	168	do	1959	162	194	do	16	26
1957	145	169	Very old	1959	159	189	do	14	20
1957	153	181	do	1959	168	202	do	15	21
1957	150	179	do	1959	169	198	do	19	19
1957	144	167	do	1959	157	189	do	13	22
1957	129	149	Old	1959	146	173	do	17	24
1957	147	172	Very old	1959	164	196	do	17	24
1957	147	166	Old	1959	162	189	do	15	23
1957	136	158	Very old	1959	154	187	do	18	29
1957	133	152	do	1959	152	178	do	19	26
1957	141	164	Old	1959	153	186	do	12	22
1957	138	160	New	1959	158	188	do	20	28
1957	142	163	Very old	1959	157	191	do	15	28
1957	169	202	do	1959	184	226	do	15	24
1957	142	160	do	1959	161	189	do	19	29
1957	143	166	do	1959	160	189	do	17	23
1957	153	176	do	1959	165	194	do	12	18
1957	153	176	do	1959	170	200	do	17	24
1957	123	138	New	1959	137	157	do	14	19
1957	137	157	do	1959	155	181	Very old	18	24
1957	144	169	Very old	1959	160	193	Old	16	24
1957	150	173	do	1959	163	194	do	13	21
1957	123	140	Old	1959	135	156	do	12	16
1958	137	159	New	1959	155	187	New	18	28

[1] Considered as two molts.
[2] Unknown.

STUDIES ON *Parorchis acanthus* (TREMATODA: DIGENEA) AS A BIOLOGICAL CONTROL FOR THE SOUTHERN OYSTER DRILL, *Thais haemastoma*

By Nelson R. Cooley, *Fishery Research Biologist*, Bureau of Commercial Fisheries

Although the biology and control of the chief Atlantic coast oyster drill, *Urosalpinx cinerea*, has been the subject of considerable study (reviewed by Carriker, 1955), the southern drill, *Thais haemastoma* Linné,[1] long known as an oyster predator, has received scant attention.

The southern drill is widely distributed in oyster-producing waters along the northern coast of the Gulf of Mexico, exists in incredible numbers in coastal bays and estuaries, and is extremely prolific. Its reproductive cycle has been studied in some detail by Butler (1953). Females deposit egg capsules regularly from March to August. Each capsule contains from several hundred to 4,000 eggs, and there is almost no mortality within the capsule. In a growth experiment performed by Butler, 250 females deposited an estimated 100 million eggs during 1 month. Hatching occurs in 12 to 16 days at 25° C, and after a planktonic life that may be as much as 7 weeks, the veliger larvae metamorphose into tiny snails. Sexual maturity is usually attained during the second summer, i.e., at 1 year of age, but normal egg and capsule deposition by snails not more than 8 weeks old has been observed.

Thais is probably the most important oyster predator in this area (Butler, 1953). In 1956 drill predation was so severe on depleted reefs in Mississippi waters (about one-half of the reef bottoms of the State) that much of the annual spatfall in the area was destroyed. In addition, drills destroyed a half of the oysters on the producing natural reefs in Mississippi that year (Chapman, 1958).

If such severe losses in the Gulf oyster industry are to be reduced, control measures must be instituted against the drill.

Broadly speaking, predation may be controlled by trapping (physical control), by poisoning (chemical control), or by parasites or predators (biological control). Physical control of *Thais* is impractical, except in restricted areas, because of expense and inefficiency of available methods. Chemical control is superficially feasible, but lack of specificity of most available chemicals raises fear of damage to oysters and other economically important species. Biological control by means of predators or parasites specific for the drill appears to be least likely to damage other species and, for that reason, was selected for investigation.

Few natural enemies of *Thais* are known. Butler's (1953) laboratory observations that hermit crabs attack drills to gain possession of their shells and that stone crabs, if sufficiently hungry, crack and eat drills are the only known proved reports of predators. The drill larva, a free-swimming veliger, may be eaten by pelagic fishes. Thus, although normal predation on larval stages may, probably does, cause enormous losses to drill populations, there appears to be no immediate prospect of further population reduction by this means.

Only a few parasites are known from *Thais*. The commensal polyclad, *Hoploplana inquilina*, and larvae of *Parorchis acanthus*, a digenetic trematode, were reported by Shechter (1943). Larval stages of at least two unidentified trematode species which caused considerable gonad damage were noted by Butler (1953).

During this study, examination of about 7,600 snails since the summer of 1956 revealed: one, possibly two, unidentified protozoans that invade and slightly damage digestive gland follicular cells; isolated instances of larval nematode infections and a few cestode infections (almost certainly larval tetraphyllideans) which appeared to be encysted single individuals, rather than reproducing populations; a single infection by sporo-

[1] Clench (1947) considers this marine snail to be two subspecies, *T. haemastoma floridana* Conrad, 1837, and *T. h. haysae* Clench, 1927, but because of ecological similarities, they are treated here as the same animal.

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cysts of an unidentified small furcocercaria; and many instances of heavy, severely damaging *Parorchis acanthus* infection. Apparently no other parasites are known.

The only immediately available prospect for development as a biological control of *Thais* appeared to be *Parorchis acanthus*, which is known to damage the drill severely and whose reported adult hosts include several species of gulls and terns occurring in this area. Therefore, a study of this parasite and its effect on the drill was initiated.

A preliminary report (1957) summarized available information on the life cycle, known hosts, morphological descriptions, synonymy and endemic localities, and gave preliminary data on experimental infection of drills, and incidence and pathology of natural infections in *Thais*.

The present paper is a final report on *P. acanthus* and gives further information on life cycle, experimental infections, and incidence and pathology of natural infections in Gulf coast drills.

Field collections of drills were made by Dr. Abraham Fleminger, then at Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas; Dr. A. K. Sparks, then at Texas A. & M. Research Foundation Laboratory, Grand Isle, Louisiana; William Demoran, Gulf Coast Research Laboratory, Ocean Springs, Mississippi; and Eugene Holzapfel and others, Aransas Pass, Texas.

William D. Wood, manager, Sanibel National Wildlife Refuge, Florida, supplied a number of young laughing gulls used in infection studies.

Consultations with Dr. H. W. Stunkard were helpful during a part of the study.

MATERIALS AND METHODS

Specimens of *T. haemastoma* from various localities in Florida, Alabama, Mississippi, Louisiana, and Texas, were examined for natural *P. acanthus* infections by dissection or by isolation in individual dishes of sea water.

For morphological studies, both living and fixed and stained material prepared by standard parasitological techniques were used.[2]

Juvenile herring gulls (*Larus argentatus*), ring-billed gulls (*L. delawarensis*) and juvenile laughing gulls (*L. atricilla*) were used as experimental hosts of adult worms. Experimental infection of gulls was accomplished as follows. Cercariae were permitted to encyst in a finger bowl of sea water and become metacercariae. The cysts, carefully scraped from the bottom of a finger bowl with a scalpel and suspended in a small amount of sea water, were pipetted directly into the stomach of a fasting bird by means of a stiff ⅛-inch-bore polyethylene tube carefully passed down the esophagus. The tube was flushed with a few milliliters of sea water and carefully removed. The bird was then returned to its cage and given its daily feeding. Alternatively, cysts or adult worms were introduced directly into the cloaca.

Attempts to infect least tern (*Sterna albifrons*) nestlings were made by feeding encysted metacercariae with a pipette immediately before giving the birds food.

All gulls were fed chopped fish that had been frozen and stored at 0° F. for several weeks to prevent infecting the birds with fish-borne helminths. Least tern nestlings were fed beef-base dog food, later supplemented with bits of fish.

If repeated examinations of cloaca and bursa Fabricii over a period of weeks were consistently negative, the gulls and terns were concluded to be free of natural infection. The same method was used to detect experimental infections, which, in most cases, were subsequently confirmed by autopsy.

Drills were infected experimentally by 24-hour exposure of individuals to freshly hatched miracidia in 4-inch bowls containing 100 ml. of sea water. These drills were kept as long as 3 days in 4-inch bowls with food and daily changes of sea water, or for periods as long as 10 weeks in battery jars with running sea water and adequate food.

Thais specimens for histological study were killed at various intervals after exposure to infection and fixed in Gilson's, Zenker's, Bouin's, or Allen's PFA–3 solutions or Smith's modification of Bouin's solution. Gilson's, Zenker's, and Allen's PFA–3 gave best results. Specimens were paraffin-embedded, sectioned at 7μ or 10μ and stained routinely by a Delafield's hematoxylin-azure B–eosin Y technique. With the azure-eosin mixture adjusted to pH 4.1 to 4.95 with McIlvaine-Lillie

[2] Fixatives: *G* (Gilson), *Z* (Zenker), *PFA–3* (Allen's PFA–3 modification of Bouin). Stains: *DH–AzB–E* (Delafield's hematoxylin–Azure B–Eosin Y), *WH–AzB–E* (Weigert's acid-iron-chloride-hematoxylin-Azure B–Eosin Y).

buffers (Lillie, 1948, p. 260–263), depending on the fixative used, the procedure produced brilliant differential staining of the two types of digestive gland follicular cells, necrotic areas in the host tissues, and various parasite-structures. In a few instances, Weigert's acid-iron-chloride-hematoxylin was substituted in the procedure, but the results were less satisfactory.

THE PARASITE

Taxonomy

The adult was originally named *Zeugorchis acanthus* by Nicoll (1906), who described it from two specimens found in the cloaca and bursa Fabricii of the herring gull (*Larus argentatus*). Following study of more material from herring and common gulls (*L. canus*), he (1907) designated it type of a new genus, *Parorchis*. Subsequently, Linton (1914) mistakenly described the same worm as a new species, *P. avitus*. Lebour (1907) described *Cercaria purpurae* from *Purpura* (=*Thais*) *lapillus* and subsequently (1914), on morphological grounds alone, correctly identified it as a larval stage of *P. acanthus*. Later, Stunkard and Shaw (1931) described *Cercaria sensifera* from *Urosalpinx cinerea* and Stunkard and Cable (1932) demonstrated experimentally that *C. sensifera* is a larval stage of *P. avitus*. Cable and Martin (1935) reduced *P. avitus* Linton, 1914, to synonymy with *P. acanthus* (Nicoll, 1906) Nicoll, 1907. To the synonym list compiled by Cooley (1957) should be added the genus *Proctobium* Travassos, 1918 (cited in Strom, 1927).

The systematic position of *P. acanthus* is illustrated by the following classification scheme taken from Hyman (1951):

Phylum Platyhelminthes
  Class Trematoda
    Order Digenea
      Family Echinostomatidae
        Genus *Parorchis* Nicoll, 1907
          Parorchis acanthus (Nicoll, 1906) Nicoll, 1907.

Morphology

The morphology of the different developmental stages of *P. acanthus* has been described by a number of authors. A complete source-list of the descriptions was given in an earlier paper (Cooley, 1957). The material of the present study is in general agreement with these descriptions. The existing differences, however, do not invalidate the identification of the present material, for, as Stunkard (1957, p. 16) pointed out, "members of a single species may differ so much as a result of development in different host species, invertebrate and vertebrate, or of different physiological conditions in host-individuals, that the extent of variation is known for few if any species. . . ."

Miracidium.—The present material is compared with published descriptions in table 1. The main differences are (1) the variation in length of anterior, body, and caudal cilia, (2) the variation in the shape of pigment spots ("eyespots," "eyes") [No two descriptions agree on this], and (3) the shorter length of the contained redia. In addition, Nicoll (1907) reported the body to be differentiated into a distinct head and a posterior part, but neither Linton (1914), Rees (1940), nor the author have observed such a condition. It was obviously a temporary shape, perhaps as a result of contraction during fixation. The miracidium swims rapidly, yawing slightly as it rotates about its longitudinal axis. While swimming, both miracidium and contained redia become elongate, but regain their typical shapes upon halting. In other respects, there is agreement with published descriptions.

TABLE 1.—*Comparison of living* P. acanthus *miracidia from several sources*

[All measurements in millimeters]

Item	Nicoll (1907)	Linton (1914)	Rees (1940)	Present study
Length (exclusive of cilia).	0.18	0.12–0.16	0.02(sic)	0.16–0.17.
Width (exclusive of cilia).	0.05	0.08	0.054	0.06–0.07.
Cilia length and disposition.	long, completely cover body.	0.02	0.015, closely set long. rows, absent on rostrum.	ca. 0.02 on body; anterior cilia shorter, stiffer, more closely arranged; caudal cilia slightly longer.
Pigment spot.	1, large, dark, usually 5-lobed.	single, distinct, black, variable shape.	kidney-shaped, 2 forming a single mass.	0–2, large black, subspherical.
Contained redia:				
Length		0.14	0.175	0.07–0.09.
Width		0.04	0.028	0.04.
Host	*Larus argentatus, L. canus.*	*L. argentatus.*	*L. argentatus.*	*L. delawarensis.*
Locality	Scotland.	Massachusetts.	Wales.	Florida.

Redia.—Specimens of this stage agree closely with published descriptions.

Cercaria.—Comparison with published descriptions (tables 2, 3) reveals slight differences which could easily result from development in a different snail host or from the fixative employed.

Most measurements of cercariae which were killed with gentle heat and measured in sea water tended to be greater than those preserved by the classic method of relaxing them by rapidly swirling in a small amount of sea water before flooding by hot fixative. The difference was due either to incomplete relaxation before fixation occurred or to agonal contraction caused by contact with fixative.

The cercariae encyst readily on any available object. Sizes of living cysts from several sources, measured in situ, are compared in table 2. The range in length and width was considerably greater in my material than in that of others. The differences which exist are most likely due to the parasites having developed in three different snail hosts.

Comparison of cyst measurements made before and after fixation revealed generally insignificant fixation-induced changes: Gilson's and Carnoy's fixatives caused slight shrinkage, while Bouin's fixative caused slight swelling.

TABLE 2.—*Comparison of living* P. acanthus *cercariae and cysts from several sources*

[All measurements in millimeters]

Item	Lebour and Elmhirst, 1922	Stunkard and Shaw, 1931	Rees, 1937		Present study
			Expanded	Contracted	
Body length		up to 0.9	1.00	0.36	0.44 –0.57
Tail length		up to 0.9	0.82	0.18	0.29 –0.61
Total length		up to 1.8	1.82	0.54	0.73 –1.18
Body width			0.09	0.35	0.21 –0.36
Oral sucker:					
Position		subterminal	subterminal		subterminal
Length		0.06–0.08 in diameter.	0.07		0.060–0.087
Width			0.01		0.067–0.107
Ventral sucker:					
Length		0.08–0.1	0.10		0.100–0.141
Width		0.1–0.115	0.11		0.087–0.121
Oral sucker: Ventral sucker		1:1.50–1:1.98	1:1.263		1:1.14–1:1.73
Cyst:					
Length	0.24–0.28	0.23–0.27	0.295 in diameter.		[2] 0.218–0.327
Width	0.20–0.22	0.20–0.23			0.185–0.294
Host	*Purpura lapillus*,[1]	*Urosalpinx cinerea*,	*Purpura lapillus*.[1]		*Thais haemastoma*,
Locality	Scotland	Massachusetts.	Wales		Florida.

[1] = *Thais lapillus*.
[2] Average of 46 cysts: 0.270 mm. *X* 0.231 mm.

TABLE 3.—*Comparison of* P. acanthus *cercariae prepared by different methods*

[All measurements are in millimeters]

Item	Stunkard and Shaw, 1931	Present study		
		Heat-killed [1]	Bouin-fixed [2]	FAA-fixed [2]
Body length	0.21–0.47	0.32 –0.88	0.21 –0.40	0.36–0.47
Tail length	0.12–0.26	0.39 –0.61	0.11 –0.48	0.28–0.47
Total length	0.33–0.73	0.71 –0.149	0.32 –0.73	0.66–0.94
Body width	0.14–0.21	0.20 –0.37	0.07 –0.21	0.11–0.13
Oral sucker: Length	0.05–0.06 (diameter)	0.054–0.094	0.034–0.060	0.03–0.06
Width		0.067–0.107	0.047–0.101	0.03–0.05
Ventral sucker: Length	0.68–0.76 (diameter) (sic)	0.094–0.147	0.047–0.074	0.06–0.09
Width		0.094–0.147	0.054–0.121	0.07
Oral sucker: ventral sucker	1:1.27–1:1.36	1:1.24–1:1.77	1:1.11–1:1.24	1:1.33–1:2.00

[1] Unstained, measured in sea water.
[2] Stained and mounted in Permount.

Adult.—Table 4 compares permanent preparations of sexually mature adults from the present study with published descriptions. No major differences exist. These data illustrate the range of variation which can result from development in different hosts.

Life Cycle

The adult was described by Nicoll (1906, 1907), Linton (1914, 1928), and Stunkard and Cable (1932).

The cercaria, described by Lebour (1907), was first found in rediae from *Purpura* (=*Thais*) *lapillus*. In 1914, after comparing it with young *P. acanthus* adults from herring gulls, she correctly inferred that *C. purpurae* is a larval stage of *P. acanthus*. Later, with Elmhirst (1922), she reported a life cycle which erroneously included a molluscan second intermediate host (either *Cardium edule* or *Mytilus edulis*).

The first correct life-history description is that of Stunkard and Cable (1932). By feeding cysts derived in vitro from cercariae naturally emitted from the oyster drill, *Urosalpinx cinerea*, to common (*Sterna hirundo*) and roseate terns (*S. dougalli*), they proved conclusively that only two hosts are necessary: a marine snail and a marine bird.

Details of miracidial structure, cercarial anatomy and encystment, and germ cell cycle in both larval and adult stages were reported by Rees (1937, 1939, 1940).

TABLE 4.—*Comparison of stained and mounted sexually mature* P. acanthus *adults from several sources*

[All measurements are in millimeters]

Item	Nicoll, 1907	Linton, 1914, 1928	Present study			
Body:						
Length	3–5	3.75–6.10	4.3–6.04	4.1–5.8	4.13–4.69	3.72.
Width	1.2–3	2.10–2.66	1.62–2.1	1.4–2.5	1.50–2.19	1.62.
Spination and spine size:						
Body	0.019–0.031×0.012		0.0356–0.0369× 0.0256–0.0335.	0.0160–0.0335× 0.0101–0.0288.	0.0268–0.0402× 0.0168–0.0201.	0.0402–0.0469× 0.0201–0.0335.
Collar	0.037	0.022	0.0201–0.0335× 0.0168–0.0268.	0.0168–0.0402× 0.0101–0.0335.	0.0235–0.0268× 0.0101–0.0134.	0.0402–0.0536× 0.0268–0.0335.
Collar number	about 60	Single row, small	57–68	54–64	71	58.
Oral sucker:						
Length	up to 0.5	0.30–0.44	0.30–0.32	0.28–0.31	0.33–0.34	0.29.
Width	up to 0.5	0.36–0.49	0.33–0.36	0.31–0.37	0.37–0.43	0.30.
Ventral sucker:						
Length	1.08	0.71–1.35	0.9–1.09	0.83–0.97	0.82–0.86	0.74.
Width	1.08	0.78–1.36	0.88–0.99	0.70–0.93	0.87–0.97	0.77.
Anterior sucker: Ventral sucker	1:2.16	1:2.86	1:2.74–1:3.30	1:2.47–1:2.92	1:2.36–1:2.43	1:2.56.
Distance of anterior margin of ventral sucker from anterior end	1.26	1.02–1.54	1.19–1.51	1.03–1.47	1.27–1.51	1.10.
Prepharynx	0.11	V. short [0.024]	0.11–0.13	0.02–0.17	0.13–0.16	0.11.
Pharynx:						
Length	0.24	0.18–0.24	0.14–0.17	0.15–0.19	0.17–0.19	0.24.
Width	0.17	0.14–0.24	0.11–0.15	0.11–0.13	0.13–0.19	0.14.
Esophagus	ca. 3x as long as pharynx [0.72].	0.36–0.52	0.33–0.44	0.30–0.60	0.58–0.73	0.44.
Testes	Lobate	Lobate	Lobate	Lobate	Lobate	Lobate.
Right testis:						
Length	0.55–0.60	0.32–1.00	0.57–0.90	0.37–0.66	0.32–0.52	0.54.
Width	0.55–0.60	0.28–0.77	0.53–0.59	0.34–0.62	0.30–0.55	0.42.
Left testis:						
Length	0.55–0.60	0.33–0.98	0.60–0.78	0.42–0.62	0.40–0.59	0.54.
Width	0.55–0.60	0.33–0.88	0.44–0.62	0.40–0.59	0.30–0.59	0.45.
Ovary:						
Length	0.33	0.15	0.16–0.22	0.15–0.28	0.20–0.28	0.18.
Width	0.25	0.24	0.17–0.26	0.17–0.30	0.24–0.38	0.24.
Egg (shape)	Elliptical	Oval	Elliptical	Elliptical	Elliptical	Elliptical.
Size, anterior part of uterus	0.106–0.113× 0.056–0.062.	0.082–0.100× 0.046–0.060.	0.0469–0.1005× 0.04–0.1038.	0.064–0.114× 0.034–0.060.	0.054–0.074× 0.027–0.034.	0.0670–0.0737× 0.0268–0.0302.
Size, posterior part of uterus	0.081–0.095× 0.040–0.044.	0.066–0.079× 0.040.	0.0603–0.838× 0.0335–0.0402.	0.064–0.104× 0.034–0.054	0.040–0.070× 0.027–0.034.	0.0670–0.0737× 0.0335–0.0391.
Miracidium	0.18×0.05, 2-part body, 1 pigment spot in head.	0.08×0.05, cilia ca. 0.02 long, 1 pigment spot in head.	0–1 pigment spot	0.16–0.17×0.06–0.07 (excluding cilia); body cilia ca. 0.02, anterior cilia slightly shorter, caudal cilia slightly longer; 0–2 pigment spots.	0–pigment spot	0–pigment spot.
Habitat	Bursa Fabricii, cloaca, rectum.	Cloaca	Cloaca	Cloaca, colon	Cloaca, cloaco-colonic junction.	Cloaca.
Host	*Larus argentatus; L. canus.*	*L. argentatus*	*L. argentatus*	*Larus delawarensis.*	*Larus atricilla*	*Sterna albifrons.*
Locality	Scotland	Massachusetts	Florida	Florida	Florida	Florida.

The essential features of Stunkard and Cable's and Rees' life cycle accounts were collated and summarized by Cooley (1957), who also compiled lists of known hosts, infection sites in each host, and localities where the parasite is endemic.

To this host list should be added the ruddy turnstone (*Arenaria i. interpres*), the natural host in Hawaii, and noddy terns (*Anous stolidus pileatus* Scopoli), sooty terns (*Sterna fuscata oahuensis* Bloxam), wedgetailed shearwaters (*Puffinus pacificus cuneatus* Salvin), and domestic ducks (Muscovy, Pekin), the last four being experimentally infectible when maintained on a diet of squid (Oguri and Chu, 1955); also the laughing gull (*L. atricilla*), a natural host in Florida, and the least tern (*Sterna albifrons*), an experimental host (present study).

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Despite the number of studies of various aspects of the life cycle of *P. acanthus*, apparently no one has described the actions of the miracidium as it attacks the drill.

Invasion of the drill by Parorchis *miracidia.*—Living miracidia are easily obtained by teasing eggs from the uterus of the adult worm into sea water. They hatch almost immediately. The hatching process is well described by Rees (1940).

The miracidium is a very rapid and active swimmer. Its restless to and fro movements seem without direction and contact with the drill appears to be accidental. However, a few observations suggest that the parasite may be attracted by the mucus secreted by the drill.

Rees (1940) stated that the position of the young first generation rediae in the digestive gland

"seems to indicate that the miracidum enters the shell aperture and makes its way up between the shell and the body of the enclosed animal. The miracidium probably penetrates the tunica propria of the digestive gland . . . and then liberates the contained redia by decomposition of itself." This sequence of events cannot be observed in the intact animal. The following observations demonstrate that it is not the sole means of entry of the parasite into the snail.

The main attack sites are the outer wall of the siphon, the base of the head, and the side (rarely, the sole) of the foot. Occasionally, miracidia, trapped in the siphonal water current, are swept into the mantle cavity. Most, if not all, pass out in the excurrent flow, but a few may possibly invade the host tissues there.

The invasion, most readily studied in the outer wall of the extended siphon, occurs in the following manner. The miracidium contacts and adheres to the skin of the drill by its anterior end. Attachment and penetration occur only when the miracidium strikes more or less at right angles to the skin surface; miracidia striking at acute angles ricochet and do not become attached.

Immediately on attachment several longitudinal contractions of the anterior two-thirds of the parasite's body follow, so that it appears to butt the snail. It quivers very rapidly for a few seconds, becomes quiescent for a short time, then a series of rhythmic contraction waves sweeps over the miracidium for approximately 30 minutes before slowing markedly. The contraction waves appear to aid penetration (fig. 1, a to e).

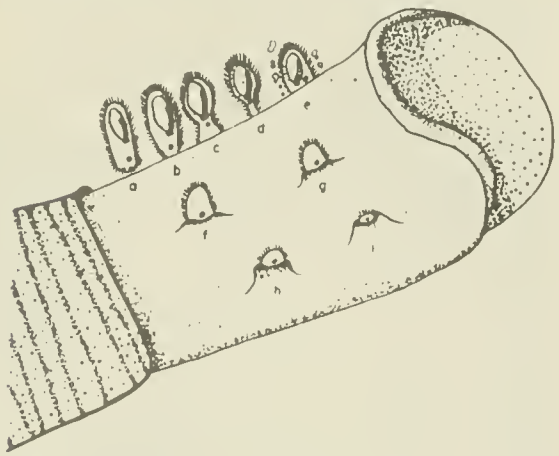

FIGURE 1.—*Parorchis* miracidia invading siphon of *Thais* (diagrammatic).

During the first 15 minutes (approximately) of the invasion, occasional small showers of host epithelial cells are carried away from the invasion site by water currents produced by the parasite's cilia (fig. 1, e). This observation appears to corroborate Rees' (1940) statement that the droplets of secretion seen by her to emerge from the two anteriorly located penetration glands onto the rostrum of the miracidium probably facilitate entry of the miracidium into the molluscan host.

About an hour after contact, the parasite's cilia appear to stop beating. Closer examination reveals that the lateral cilia continue to beat very slowly for at least another half hour as the miracidium moves in and out of the low wheal which develops at the invasion site and progressively enlarges as the miracidium penetrates deeper into the snail (fig. 1, g to i).

In about 1½ hours after attachment, the first generation redia contained in the miracidium could no longer be seen. Whether the redia has left the miracidium and entered the host tissues or still lies within the miracidium could not be ascertained.

Complete penetration by the miracidium requires about 6 hours. The subsequent fate of the miracidium is unknown, but it is presumed to disintegrate completely within the host, since no trace has been found in serial sections of snails fixed as early as 24 hours after penetration was known to have occurred. Nor was Rees (1940) able to find any trace of it either inside or outside the snail host. On the other hand, the miracidium of *P. acanthus* may behave in the manner described by Stunkard (1934) for *Typhlocoelum cymbium*, whose miracidium does not penetrate the snail. After that miracidium is securely attached and partially embedded, the redia leaves it and enters the snail.

Peculiarly, as the miracidium penetrates deeper, its eyespot seems to move posteriorly until it lies in the rearmost part of the parasite's body (fig. 1, e to i). The reason for the apparent rearward migration of the eyespot is uncertain, but it is probably related in some way to the escape of the redia from the miracidium.

Redial Development.—The young, first-generation redia has not yet been demonstrated at the

invasion site itself. At 24 and 72 hours after drills were first exposed to numerous miracidia, very young first generation rediae were found in the tissues of the head and columellar muscle as well as in the arteries, veins, sinuses and tissues of the siphon, foot, eyestalk, mantle, kidney, and visceral mass (figs. 2, 3, 5.)

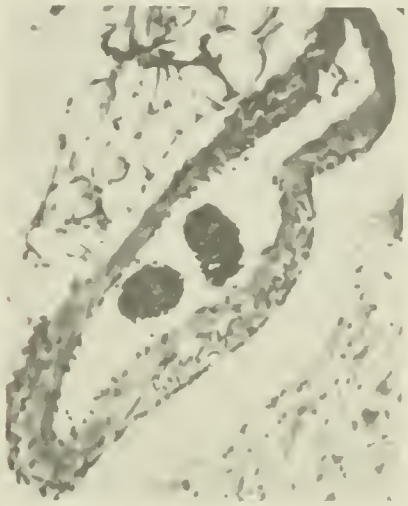

FIGURE 2.—Very young redia in large vein next to columellar muscle; 24-hour experimental infection; G, DH–AzB–E; X210.

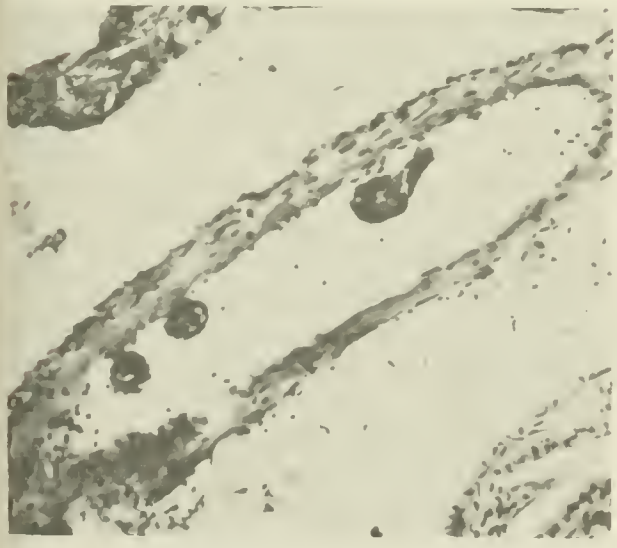

FIGURE 3.—Very young redia, parts of two others, in large vein near digestive gland, 72-hour experimental infection; PFA–3, DH–AzB–E; X210.

FIGURE 4.—Much older redia in renal blood sinus; natural infection; Z, DH–AzB–E; X215.

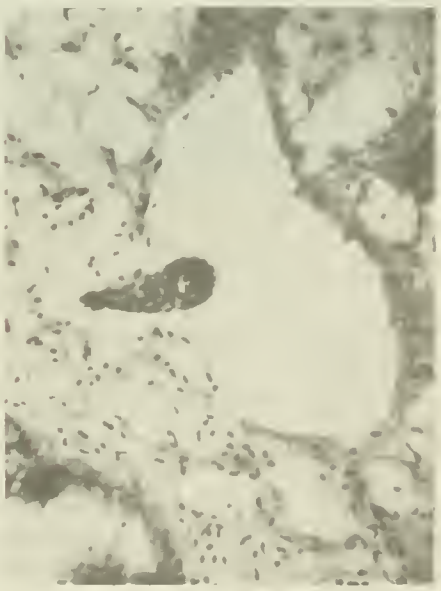

FIGURE 5.—Very young redia entering sinus in siphon wall; 72-hour experimental infection; PFA–3, DH–AzB–E; X210.

By the eighth day, the rediae had grown markedly and germ balls (embryos of the next larval generation) had begun to appear internally, (fig. 4), but the rediae were still found in much the same locations as during the first three days of infection.

Ten weeks (November to February) after a small drill was exposed to about 50 miracidia, serial sections revealed 15 well-developed rediae in the head, foot, visceral mass, in the aorta near the heart, and, for the first time in this study, in the anterior margin of the digestive gland, favorite site in heavy natural infections. Most of the rediae contained daughter rediae which, in turn, contained germ balls of a third generation (fig. 6). This degree of development is probably

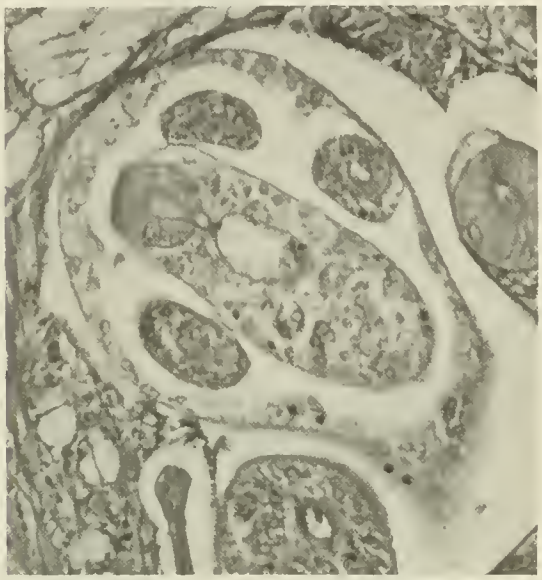

FIGURE 6.—Redia with daughter rediae, one of which contains germ balls of a third generation, in foot: 10-week experimental infection; G, DH–AzB–E; X230.

attained sooner at the higher water temperatures prevailing during spring and summer.

The entrance of rediae into the digestive gland marks the beginning of a concentration of parasites there, as is found in natural infections.

Rees (1940) notes that the parent (first generation) redia gives rise to 20 or more daughter rediae and that daughter rediae produce only cercariae. If daughter rediae produce only cercariae, it would appear that the parasites would complete their development in a relatively short time and depart, leaving the snail host infection-free. However, the present study has demonstrated that natural infections persist for at least 2 years.

Sections of snails harboring natural infections known to be at least 2 years old always had large numbers of daughter rediae containing cercariae in various stages of development. Although no daughter rediae containing recognizable rediae were found, there were occasional small rediae containing embryos which might have developed into either rediae or cercariae. The evidence suggests that there occurs a series of redial generations before final production of cercariae.

Observing the prominent procuscula (posterior "feet") of young rediae and their considerable activity when removed from the snail, Rees (1940) concluded that the rediae are capable of migrating among the follicles of the digestive gland. The present study demonstrates rediae in various stages of development in a wide variety of lodgment sites, the location of which depends on how long the snails have been experimentally infected. In addition, rediae whose intestines contained yolk platelets have been found in the digestive gland of a naturally infected snail (fig. 9), indicating that they had migrated from the ovary into the digestive gland. It can be concluded, therefore, that the redia is capable of migrating from an invasion site anywhere on the body of the snail to the final lodgment in the digestive gland or gonad.

Although all experimental drills kept alive for more than 3 days were maintained in running sea water with adequate food to keep them in good physiological condition, it is highly improbable that any could have become infected by miracidia brought in by the incoming sea water; because, although simultaneously supplied by the same salt water tap, none of the control snails of these experiments, and none of 27 control drills of a longevity study of *Parorchis*-infected drills similarly maintained for more than 2 years, ever became infected by *Parorchis* or any other trematode.

Cercarial Encystment.—The swimming and creeping motion of the cercaria was described by Stunkard and Shaw (1931), who noted that it attached readily to any surface and encysted soon after attachment. In the present study, however, the cercariae usually alternated between attachment and creeping or swimming many times before finally encysting.

Accelerated encystment following either mechanical stimulation, such as stirring or shaking, or chemical stimulation, such as use of too concentrated solutions of vital dyes, was noted by

Stunkard and his coworkers (1931, 1932). This finding has been confirmed in the present study. Under these conditions, the cercaria encysted almost immediately upon contacting the substratum.

The encystment process was described briefly by Stunkard and Cable (1932), more fully by Rees (1940). My own observations amply confirm their findings. However, the following observations should be added to their descriptions. About 1 minute after extrusion of the cystogenous material, the body rapidly shrinks, withdraws into the center of the cyst and becomes immobile. The shrinkage and withdrawal results in decaudation. The detached tail, now attached by its base to the outer cyst membrane, lashes about for several hours. After some hours, the body begins to move about within the cyst membranes and ultimately assumes the characteristic folded position figured by Stunkard and Cable, and by Rees.

NATURAL INFECTIONS IN *THAIS*

Incidence

The incidence of natural infections of *P. acanthus* in *T. haemastoma* examined between July 1956 and September 1959 is summarized in table 5. Although the parasite is widely distributed along the Gulf coast, the infection rate in any sampled locality was low. The apparent absence of infections in snails from Apalachicola Bay, Florida, and Port Aransas, Texas, and the low rates in drills from Dauphin Island Bay, Alabama, and Barataria Bay, Louisiana, may be due to small sample-size or, possibly, to more resistant snail populations or fewer infected birds in those localities.

The following data suggest that the drill infection-rate in a given locality may be higher on the feeding grounds of the local gull population than at a site away from them. Between June 1958 and June 1959, 5.37 percent (57 of 1064) of the drills collected at a site on the north shore of Pensacola Bay, Florida, had *P. acanthus* infections, but only 0.47 percent (4 of 859) of those from a site on the south shore were infected. Although these two sites are only 3.5 miles apart, similar marked differences in incidence of infection have been observed in all collections made there since the summer of 1956 and appear to be correlated with the high concentration of gulls at feeding grounds on the north side of the bay.

TABLE 5.—*Incidence of natural infections of* P. acanthus *in* T. haemastoma, *1956–59*

Locality	Snails		
	Number examined	Infected	
		Number	Percent
Alabama:			
Dauphin Island Bay	383	1	0.26
Florida:			
Apalachicola Bay	138	0	0
Pensacola Bay	3,874	105	2.71
Santa Rosa Sound	691	8	1.15
Total	4,703	113	2.40
Louisiana:			
Barataria Bay	357	1	0.28
Mississippi:			
Mississippi Sound	700	29	4.14
Texas:			
Galveston Bay	1,277	45	3.52
Port Aransas	184	0	0
Total	1,461	45	3.08
Grand total	7,604	189	2.48

Pathology in the Snail

Stunkard and Shaw (1931) and Stunkard and Cable (1932) noted that infected *Urosalpinx cinerea* and *Thais* [=*Purpura*] *lapillus* in Massachusetts harbored *P. acanthus* larvae in the interlobular spaces of both digestive gland and gonad. The picture was similar in both species: the uninfected snail had a plump visceral mass, yellow digestive gland, and cream-colored gonad, whereas the parasitized snail had shrunken organs and lighter colored body, and its gonad might have been destroyed.

Rees (1937) noted the parasite in the same organs in *Thais* [=*Purpura*] *lapillus* in Wales and reported a similar picture, except for finding the visceral mass of the parasitized snail much swollen.

Menzel and Hopkins[3] noted that many old *Thais haemastoma* from Barataria Bay, Louisiana, had heavy infections of *P. acanthus* larvae, which destroyed the gonads and caused complete sterility. Hopkins's (1957) report appears to be the earliest published record of *Parorchis*-induced castration of *T. haemastoma*. The following pathology study, part of which confirms their observation, had already been completed before the writer learned of their findings.

[3] Menzel, R. W., and S. H. Hopkins, 1954. Studies on oyster predators in Terrebonne Parish, La. Mimeographed report, Texas Agricultural and Mechanical Research Foundation, College Station, Texas. (Released, 1959).

Data obtained more recently from examination of 189 naturally infected drills collected in all seasons from 1956 through 1959 require revision of my earlier (1957) brief description of the pathology of drill infection.

The digestive gland of the uninfected drill is variable in color, usually light gray or beige, but may be very dark, almost black; it has a soft, cheesy consistency, and is covered by a fairly tough tunica propria. The digestive gland of the infected drill is less variable in color, usually lighter gray or light yellow, is swollen, has a softer consistency and a more easily torn tunica propria, through which can be seen enormous numbers of rediae scattered among widely separated small masses of host tissue.

The gonads of uninfected drills vary in size and thickness with seasonal changes in reproductive activity, but the color is usually brownish in males and yellow to orange in females. In infected drills, the gonad is thin and patchy, or completely absent; when present, its color is cream to brown in males and usually yellow to orange, sometimes brownish, rarely oyster white, in females.

Sex determinations were made on approximately one-half of all infected snails (98 of 189) collected in the present study; the sex ratio of these snails was approximately one male to 1.6 females. It is found, even in small lots of drills, that a 1 : 1 sex ratio usually prevails in field collections.

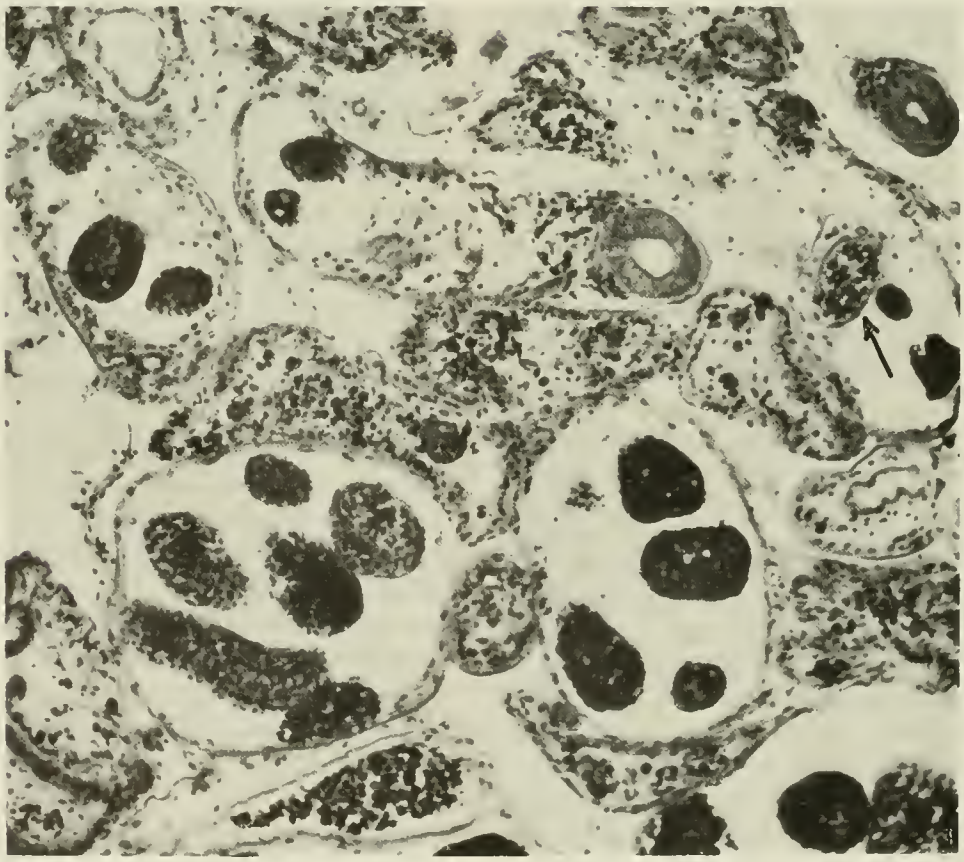

FIGURE 7.—Daughter rediae in various stages of development in ovary, natural infection; Z, DH–AzB–E; ×212.

FIGURE 8.—Redia with yolk platelets in posterior end of intestine (arrow), digestive gland, natural infection: Z. WII-AzB-E; ×215.

Microscopic examination of stained sections of infected drills reveals:

(1) Extensive destruction of the digestive gland, due to redial ingestion of host tissue, which may reduce intact tissue to 10–30 percent of the area of a cross section of the gland; (2) Compression of the remaining digestive gland tubules with resultant obliteration of most, if not all, lumina because of growth of the large number of rediae; (3) Basophilic inclusion granules of uncertain significance in the cytoplasm of the large triangular cells of the digestive gland; (4) Amoeboid cells, thought to be phagocytic blood cells, grouped about some rediae in the digestive gland; and (5) Gonadal damage which is directly related in extent to severity of infection, massive infections resulting in severe to total destruction due to ingestion of host tissue by rediae (figs. 7–10).

Naturally acquired *Parorchis* infections produce lasting damage. Forty-four infected drills maintained in an aquarium with running sea water and adequate food did not spawn during an entire breeding season, and 26 of these failed to spawn during a second breeding season (approximately 2 years in captivity), the remainder having been sacrificed for various purposes. Similarly maintained control snails spawned normally each year.

Duration of Infection

It is not known precisely how long these infections last, but 26 naturally infected drills maintained in the laboratory for 2 years regularly emitted cercariae when tested and all were heavily infected when sacrificed for dissection or for histological study. Thus, once established, the

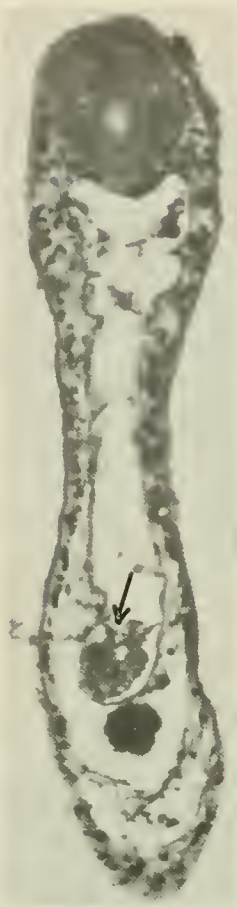

FIGURE 9.—Daughter redia in ovary showing yolk platelets (arrow) and developing cercariae, natural infection; PFA-3, DH-AzB-E; ×215.

infection persists for 2 years and possibly for the life expectancy of the snail, estimated by Butler (1953) to be 5, possibly as much as 10, years.

EXPERIMENTAL INFECTIONS

Adult Hosts

Juvenile herring (*Larus argentatus*), ring-billed (*L. delawarensis*), and laughing gulls (*L. atricilla*), and nestling least terns (*Sterna albifrons*), all common along the Gulf coast, were tested for suitability as reservoir hosts for disseminating *P. acanthus* among wild drill populations.

The observed incidence of natural *P. acanthus* infection in these species is given in table 6. It is noteworthy that some individuals of all three gull species were naturally infected. Absence of

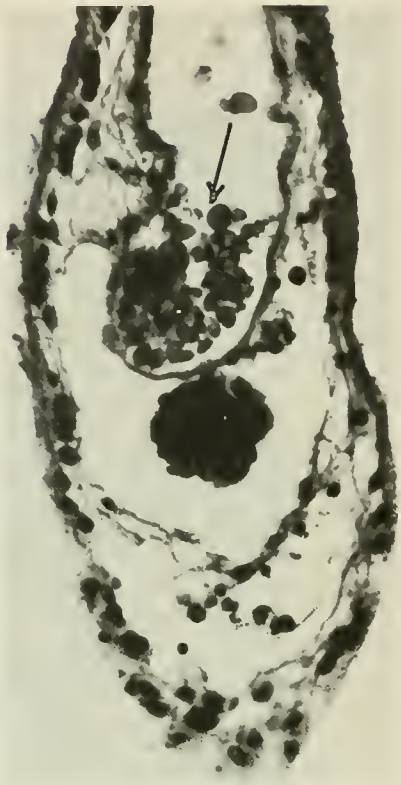

FIGURE 10.—Same redia, ×450.

infection in the least tern nestlings was expected, since they were no more than a day old when obtained and had not been exposed to infection in the laboratory.

Experimental infections were established by two methods: oral or anal administration of encysted metacercariae and transfer of mature or immature adult worms by pipette to the cloaca of an uninfected bird.

TABLE 6.—*Incidence of natural* P. acanthus *infections in juvenile gulls and nestling least terns*

Species	Number examined	Infected		Number of worms recovered
		Number	Percent	
Herring gull	18	4	22.2	17
Ring-billed gull	12	3	25.0	3
Laughing gull	31	4	12.9	4
Least tern	8	0	0	0

The results of oral administration of cysts are given in table 7. The data show that juvenile herring and ring-billed gulls were readily infected, juvenile laughing gulls were less susceptible, and nestling least terns were resistant.

There are no data to explain why some juvenile laughing gulls should become naturally infected, while others of the same age in the same colony and free of natural infection could not be infected experimentally. Possibly some significant, but unknown, difference between naturally encysted metacercariae and those which have encysted in the 4-inch bowls of sea water prevents the latter from infecting laughing gulls. Neither is it possible to explain the observed resistance of least terns. Perhaps least terns are less susceptible to *Parorchis* infection than were the common and roseate terns used by Stunkard and Cable (1932).

Encysted metacercariae were given per anum to a single herring gull on two occasions 18 days apart. It became infected after the second dose and yielded 19 mature worms at autopsy.

TABLE 7.—*Susceptibility of marine birds to experimental* P. acanthus *infection by encysted metacercariae given orally*

Species	Cysts given once		Cysts given twice		Totals	
	Number tested	Number infected	Number tested	Number infected	Number tested	Number infected
Herring gull	4	2	3	3	7	5
Ring-billed gull	4	4	1	1	5	5
Laughing gull	3	[1] 1	1	0	4	1
Least tern	2	0	---	---	2	0

[1] Fed two metacercariae naturally encysted on a Xanthid crab; all other birds fed metacercariae which had encysted on bottom of a glass bowl.

Transfer of adult worms was successful only once. A single sexually mature worm was transferred from a laughing gull to a young least tern and was recovered alive when the tern died a week later. Three other transfers failed to establish infections in the recipient: Herring gull to herring gull, 13 immature worms; herring gull to herring gull, 58 immature worms; and herring gull to ring-billed gull, 16 mature worms. It is not known why these transfers failed to infect. Possibly, the recipient gulls possessed a local immunity which caused rejection of the inocula. It is also remotely possible that the recipients could have gained immunity via a pre-existing infection since they were wild birds. But since the birds were all still immature, it seems unlikely that such infections could have been lost quickly. Further, direct visual examination of the cloacae made repeatedly over a period of several weeks prior to the transfers failed to reveal any *Parorchis* infection and none was found at autopsy.

To obtain a measure of the intensity of infection which might be expected to develop in host birds, 9 gulls were given known numbers of encysted metacercariae orally, and the numbers of adult worms developing in resultant infections were determined. Table 8 shows that only about one-half of the birds became infected. In successful infections generally only a few of the encysted metacercariae developed into adult worms.

The yield of adult worms was also low among six other gulls, not shown in table 8, which earlier were fed large, but undetermined numbers of *Parorchis* cysts in order to obtain worms and eggs for use in drill infection studies. One herring gull yielded five worms. Two of five ring-billed gulls yielded one worm each; the other three yielded two worms each.

LARVAL HOSTS

The results of drill-infection experiments are given in table 9. Nearly 60 percent of all experimental drills became infected. The small number of rediae recovered in serial sections of infected drills indicates that most of the miracidia failed to penetrate drills and consequently, the intensity of infection in individual drills was very low. This very low intensity of the experimental infections might be interpreted to suggest that repeated exposure to infection would be required in order to build up intensities comparable to those found in individual wild drills. However, the observed incidence of natural infections was so low that it appears more likely that the high intensities observed in natural infections are the result of multiple exposure, i. e., *simultaneous* exposure to many miracidia, rather than of repeated, or sequential exposures.

TABLE 8.—*Relation of* P. acanthus *adults recovered to encysted metacercariae given orally in gull infection experiments*

Species	Cysts fed (approx.)	Worms recovered	Percent recovery	Remarks
Cysts given once:				
Herring gulls (4)	128	9	7.03	Immature (12 days).
	250	0	0	
	750	0	0	
	1,000	70	7.00	Immature (11 days).
Laughing gulls (3)	[1] 2	1	50.00	Sexually mature (21 days).
	62	0	0	
	100	0	0	
Cysts given twice:				
Herring gulls (2)	250	1	0.13	Sexually mature (5½ months).
	500	0	0	
	1,640	1	0.06	Sexually mature (20 days).
	3,300	130	3.94	Immature (5 days).

[1] Metacercariae naturally encysted on Xanthid crab leg.

TABLE 9.—*P. acanthus infections developing in* T. haemastoma *exposed to freshly hatched miracidia in 4-inch bowls for 24 hours*

Drills		Number of Miracidia	Infected		Number of rediae recovered
Number	Size (mm.)		Number	Percent	
4	13–35	20–50	3	75	4, 6, 16–19
2	10, 19	50–75	2	100	3, 19
5	25	100–150	1	20	2
3	6–10	50	2	66.7	2, 15

DISCUSSION AND CONCLUSION

Heavy natural *Parorchis acanthus* infections destroy the gonad of *Thais haemastoma* thereby reducing its reproductive potential. This method was thought to offer a possible means of controlling the size of drill populations; however, in all wild drill populations sampled in the present study, the infection rate was low. Incidence of infection was also low in gulls, definitive hosts of the parasite. Since the two infection rates are closely related, it would appear that an increase in the number of infected gulls in a given locality would increase the drill infection rate and thereby tend to obtain a measure of control over the drill population-size. This is more difficult to attain than is at first apparent.

Given a good definitive host-species as a source of supply, successful dissemination of the parasite among members of a wild drill population depends, in part, on the numbers of miracidia released in the vicinity and, in part, on the numbers of miracidia actually infecting drills. The former depends on the intensity and rate of infection in local gulls, the latter on opportunity of the miracidia to contact drills and on susceptibility of the drills to infection.

The generally low intensity attained in experimentally induced gull infections, despite administration of large doses of cysts, suggests that very large numbers of gulls would have to be infected and released nearby in order to provide a significant increase in the number of miracidia available to infect drills of a given population. This constitutes, in my opinion, a serious obstacle to successful employment of *P. acanthus* in drill control.

Some evidence suggests that, in a given locality, the pattern of distribution of naturally infected drills may be correlated with the concentration of gulls on feeding grounds. Thus, drills not living on or near the feeding grounds would be less likely to become infected. This may be a factor contributing to the maintenance of the low natural infection rates observed in Gulf coast localities and would have to be dealt with in order to increase infection rates and reduce the size of drill populations.

Some laboratory experiments suggest that susceptibility of uninfected drills to *P. acanthus* is considerably higher than natural rates would lead one to suspect. If true, this would indicate that an as yet unrealized capacity for higher infection rates probably exists in wild drill populations. This capacity cannot be realized in a given drill population until larger numbers of miracidia are available in its vicinity.

The present study has found no effective means of spreading the parasite in increased numbers. With the available avian hosts and techniques, there is no evidence that infection rates can be significantly increased in wild drill populations. Therefore, the conclusion is inescapable that, using these methods, *P. acanthus* cannot be employed as an effective biological control of the drill, *Thais haemastoma*.

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DEVELOPMENT OF EGGS AND YOLK-SAC LARVAE OF YELLOWFIN MENHADEN

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The menhadens, genus *Brevoortia*, inhabit the coastal waters of the western Atlantic Ocean from Nova Scotia to central Argentina and support the largest commercial fishery in the United States, yet their early developmental stages are little known. Kuntz and Radcliffe (1917) described developing eggs, yolk-sac larvae, and older larvae identified as Atlantic menhaden (*B. tyrannus*). Based on their descriptions, Atlantic menhaden eggs and larvae have been reported from Chesapeake Bay (Pearson, 1941), Long Island Sound (Perlmutter, 1939; Wheatland, 1956; Richards, 1959), and Narragansett Bay (Herman, 1959). Eggs, tentatively identified as Atlantic menhaden, were obtained off the North Carolina coast in November and December, 1956 and 1957 (Reintjes).[1] In 1957 eggs were hatched in the laboratory, but the larvae died after the yolk sac was absorbed.

Menhaden eggs and larvae were reported from plankton collections made off the south Atlantic coast of the United States during three cruises of the motorship *Theodore N. Gill* (Reintjes, 1961), but no identification to species was made. Although the foregoing observations provided a description of eggs and larvae and information on their distribution, some question remained as to whether these actually were menhaden.

The absence of spawning, or running-ripe, fish in the landings has precluded mechanical fertilization and rearing of the eggs and yolk-sac larvae for the identification of Atlantic menhaden (*B. tyrannus*) and Gulf menhaden (*B. patronus*), the two species of principal commercial importance. The occurrence of spawning yellowfin menhaden (*B. smithi*) in the landings of a gill-net fishery at Sebastian, Fla., made possible the distinction of eggs and yolk-sac larvae of this species from those of other clupeoid fishes. Development of embryos and larvae was followed and described from the time of fertilization until absorption of the yolk.

The procedures of the work were: (1) obtain ripe ova and sperm from freshly caught yellowfin menhaden, (2) effect fertilization by mixing the sex products, (3) hold fertilized eggs in a suitable environment at known temperature during development, (4) remove and preserve examples of developing eggs and larvae, (5) observe the properties of eggs and the behavior of early larvae, and (6) collect planktonic eggs and larvae concurrently for comparative material.

MATERIALS AND METHODS

Beginning in November 1959 weekly samples of adult yellowfin menhaden were obtained from gill-net landings at Sebastian, Fla., to follow maturation of ovaries and testes. Each sample consisted of about 100 fish taken at random from the catch. Free-flowing milt was observed from cut testes in mid-December, and on January 11, 1960, several females in the sample extruded ova when pressed firmly. Each week thereafter, the number of fish apparently ready to spawn increased. On February 8, approximately one-fourth of the females and all of the males appeared ready to spawn.

On February 12, a temporary field laboratory was set up in a small dockside building at Sebastian, Fla. Equipment included compound and dissecting microscopes, thermometers, salinometers, small dip nets, one-half-meter plankton nets, an assortment of glass preparation bowls and polyethylene containers, and pens with nylon-net compartments. Other than the pens, no other equipment of special construction was used.

For rearing purposes, two pens, or enclosures, were constructed, following the design of the blue crab shedding floats, or live-cars, used throughout the Chesapeake Bay and middle Atlantic region

[1] Eggs and yolk-sac larvae of Atlantic menhaden. Unpublished manuscript. U.S. Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.

NOTE.—Approved for publication June 28, 1961. Fishery Bulletin 202.

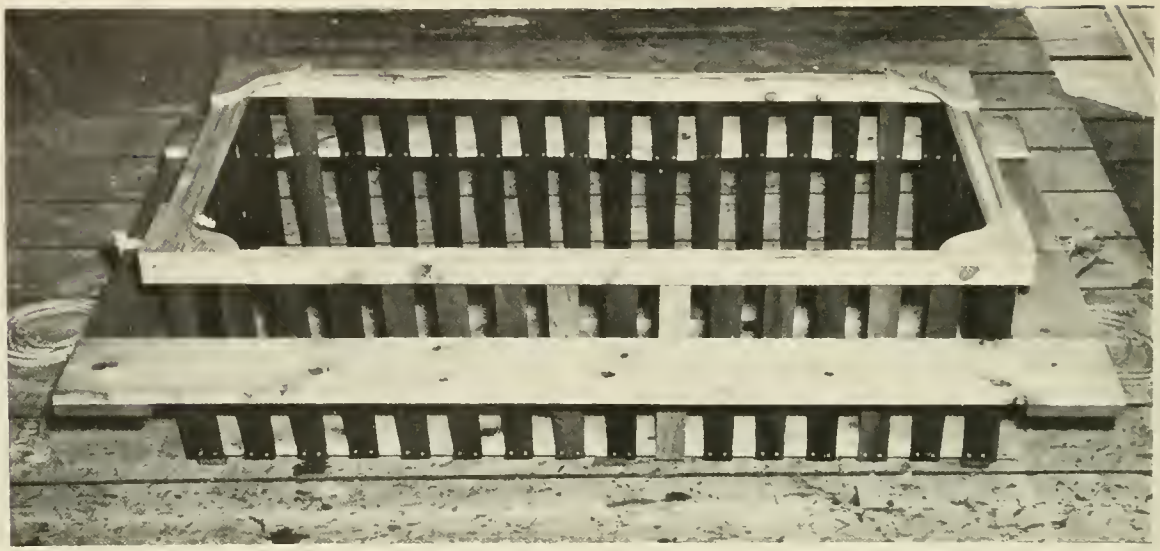

FIGURE 1.—Pen used to confine yellowfin menhaden eggs during development.

FIGURE 2.—Pen with nylon-mesh compartments floating in Indian River, Fla.

(Wharton, 1954). The pens were made of juniper boards and cedar slats (fig. 1). The dimensions were as follows: 18 inches high, 62 inches long, and 32 inches wide, with a 5-inch flange on all four sides. The flange regulated the submergence depth of the pen and provided stability.

Compartments, made of woven-mesh nylon netting, were used to confine the fertilized eggs and larvae within the pens. Two compartments were made of mesh with an average opening of 0.5 mm., and two compartments were made of mesh with an average opening of 1.0 mm.[2] All seams reinforced with nylon binding tape. The compartments were enclosed, except for access along one side (fig. 2). Because the access slit gaped during rough weather and allowed debris to enter and eggs to escape, a plastic slide fastener later was added. Each pen held two compartments that were kept in place by a tie at each corner.

Yellowfin menhaden used in the fertilization trials were obtained from gill-net catches made within sight of the temporary field laboratory. Usually, the nets were set at dusk and picked up about an hour later. Ripe females with extruded ova, or greatly distended abdomens, were removed and set aside while the net was being recovered. Males producing milt with viable sperm commonly occurred in the catch. Ripe females, on the other hand, were rare, for only 25 gravid females were found among approximately 4,000 fish examined. For all attempted fertilizations, fish were dead less than two hours.

Fertilization was accomplished by mixing ova and sperm obtained by pressing the sides of the fish, or by cutting open the ovary or testes to free the mature sex products. The ova and sperm were mixed "dry," i.e., without sea water. Dockside water was filtered through cotton to remove organisms including fish eggs and then added. The criterion of fertilization was the formation of a wide perivitelline space.

Fertilized eggs were placed in the mesh compartments of the floating pens and in glass or polyethylene containers in the laboratory. Samples of the developing embryos were removed periodically from the floating pens and placed in the laboratory containers. Development was observed with a microscope, and samples were removed and preserved in 5 percent formalin.

[2] One hundred percent Dupont nylon pattern No. 109 (0.5 mm.) and pattern No. 1400 (1.0 mm.).

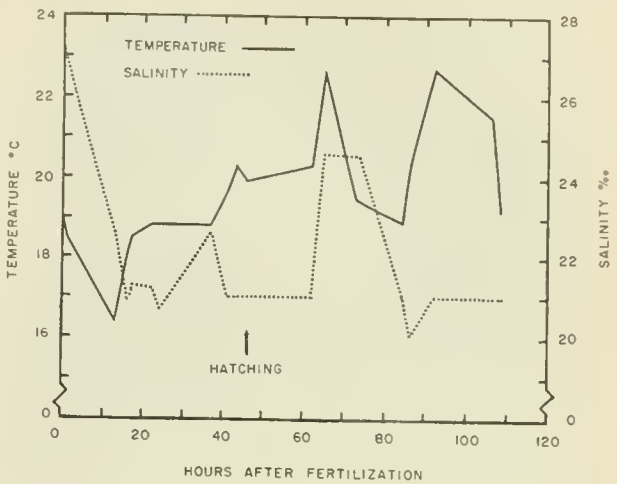

FIGURE 3.—Fluctuations of temperature and salinity during the development of eggs and yolk-sac larvae of yellowfin menhaden.

The time required for development of the embryo was recorded as age-in-hours from manual fertilization and for the yolk-sac larva, from the time of hatching. The water temperature of Indian River, immediately adjacent to the dock and rearing floats, and of the culture bowls was recorded at infrequent intervals during development (fig. 3). The observed temperature ranged from 16.4° C. to 22.7° C., with a mean of 19.6° C.

Salinity was determined at each temperature observation. The observed salinity ranged from 20.1‰ to 27.2‰, with a mean of 22.1‰.

Plankton collections of yellowfin menhaden eggs and larvae developing under natural conditions were obtained in the Indian River. Ten-minute tows were made with a half-meter net in the vicinity of the gill-net fishing grounds near Sebastian Inlet, and at one mile intervals for a distance of 6 miles north and 12 miles south of the inlet. Developing eggs from the plankton collections were used for the photographs of several stages not obtained during the development of artificially fertilized eggs. Although the size and appearance were similar to eggs of known origin, there were slight differences that are without adequate explanation. However, the identity of the planktonic eggs was assumed because of structural similarities and the concurrence of spawning yellowfin menhaden in the immediate vicinity.

DESCRIPTION OF FERTILIZATION TRIALS

Sixteen manual, or artificial, fertilizations were attempted to obtain developing embryos from positively identified yellowfin menhaden. A single female and several males were used in the first trial. The ova were removed by dissection, divided into three lots, and those in each lot mixed dry with milt from a separate male. Fifteen minutes later, filtered dockside water (salinity 20.5°/oo, and temperature 20.1° C.) was added to each container. An hour later, approximately 90 percent of the eggs in one lot were fertilized. The other two lots contained so few fertilized eggs, perhaps because of less viable sperm, that they were discarded. Development was arrested after several hours during early cleavage. Whether the failure to develop was due to decomposition, stagnation, or immaturity of ova or sperm could not be determined.

Four females were used in the second trial. Ova were removed by dissection, mixed "dry" with milt, and 15 minutes later, dockside water was added (27.2°/oo, 19.0° C.). The apparent success of fertilization varied from 40 to less than 10 percent. Two lots of eggs were placed in the floating pen anchored off the end of the dock where salinity was 26.7°/oo and temperature 18.5° C. The remaining two lots were placed in containers in the laboratory. Twelve hours later, eggs in the laboratory containers had failed to develop beyond early cleavage and showed signs of decomposition. Samples of eggs from the pens appeared normal, although in one compartment, few ova were fertilized. This trial furnished most of the developing embryos and yolk-sac larvae used for the descriptions.

DESCRIPTION OF EGG

Living eggs showed an iridescent, glasslike transparency, with little or no color in the yolk. Iridescence disappeared when the material was placed in formalin, but the chromatophores were retained and accentuated as the developing embryo and yolk became clouded. The following description is based on preserved material.

The egg is spherical and has a resilient, transparent membrane. Under magnification of 100 diameters or more, the membrane surface is marked with fine, short lines that form no discernible pattern. The yolk is segmented, contains a single oil globule, and is pale yellow. The oil globule is near the vegetative pole and floats uppermost throughout development. Coarse granulation of the yolk appeared to be characteristic of eggs not fully matured.

Comparative measurements showed the planktonic eggs to be slightly larger than those obtained artificially (table 1). Fertilized eggs in the plankton, similar in appearance and structure to those artificially fertilized, were assumed to be from yellowfin menhaden. Whether the artificially fertilized eggs had not reached maximum size because of immaturity, or whether naturally spawned eggs swell to a greater size could not be determined. Eggs, ranging from approximately 1.0 to 1.1 mm. in diameter, developed a fertilization membrane and perivitelline space; however, the very low fertility and the failure of most eggs to develop beyond the earliest stages of cleavage indicated that these ova had not reached maturity.

TABLE 1.—*Measurements of yellowfin menhaden eggs, in millimeters*

Item	Planktonic eggs (N=200)		Artificially fertilized eggs (N=50)	
	Range	Mean	Range	Mean
Fertilized egg	1.21–1.48	1.34	1.15–1.30	1.22
Perivitelline space	.33– .50	.42	.34– .46	.39
Yolk	.77–1.04	.90	.77– .95	.86
Oil globule	.05– .18	.13	.07– .16	.13

Developing yellowfin menhaden eggs from the plankton were buoyant, floating just beneath the surface film. Unfertilized eggs rested on the bottom in still water. Artificially fertilized eggs formed a layer above the unfertilized eggs, floating off the bottom with the slightest disturbance.

DEVELOPMENT OF THE EMBRYO

In discussing the development of yellowfin menhaden eggs the following three stages are used (Ahlstrom and Counts, 1955):

Early—from fertilization to closure of the blastopore.

Middle—from closure of the blastopore to the time that the separating tail begins to curve laterally away from the embryonic axis.

Late—from the time the tail curves away from the embryonic axis to the time of hatching.

EARLY-STAGE EGG

The perivitelline space developed and widened within 15 minutes after ova and sperm were mixed in sea water. If the ova and sperm were mixed in the absence of water, the perivitelline space was not readily apparent until after sea water had been added. Unfertilized and fertilized eggs from the same lot, one hour after the sex products were mixed, are shown in figures 4 and 5.

Early cleavage was rapid, and a layer of cells was formed by the 7-hour stage (fig. 6). Continued cell division resulted in the formation of a dome-shaped blastodermal cap on the yolk (fig. 7) after 12 hours. Eggs collected from the plankton (fig. 8) showed the blastodermal cap covering nearly one-third of the yolk. These late blastula were estimated as 14 hours old.

FIGURE 4.—Unfertilized egg of yellowfin menhaden.

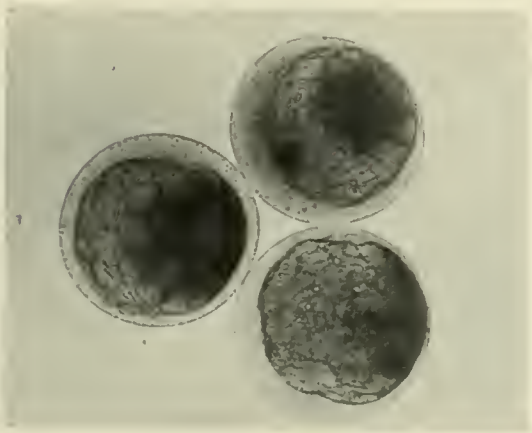

FIGURE 5.—One-hour stage with perivitelline space.

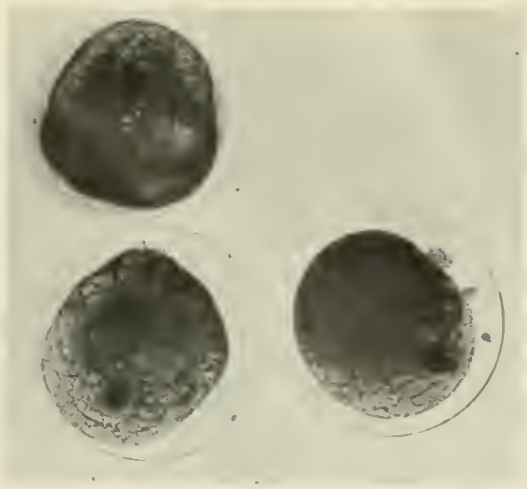

FIGURE 6.—Seven-hour stage with early cleavage.

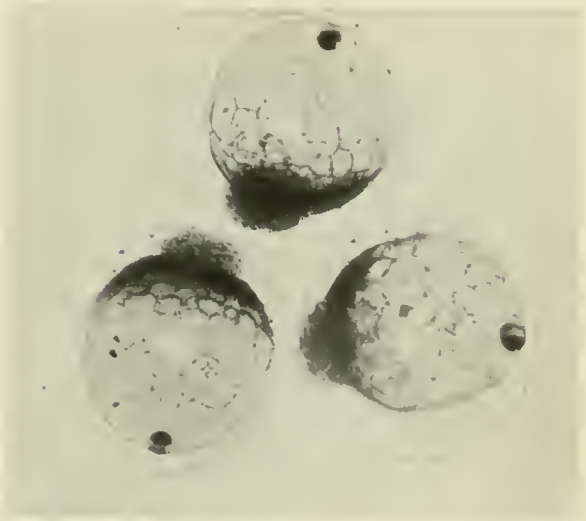

FIGURE 7.—Twelve-hour stage with blastodermal cap.

Some of the early stages showed yolk diffusion into the perivitelline space (fig. 9). This was assumed to be due to mechanical rupture of the yolk membrane during the handling and preservation of the eggs, since yolk encircled by the blastoderm in later stages did not appear to be ruptured (figs. 10, 11, 12, and 15).

At the late blastula stage the blastodermal cap, now known as the embryonic shield (fig. 9), had developed. The early embryo could be seen as a medial thickening of the shield. The peripheral cells continued to spread over the yolk surface.

The early neurula marked the end of the early-stage egg (fig. 10). The developing embryo, with a discernible head and several myomeres, became

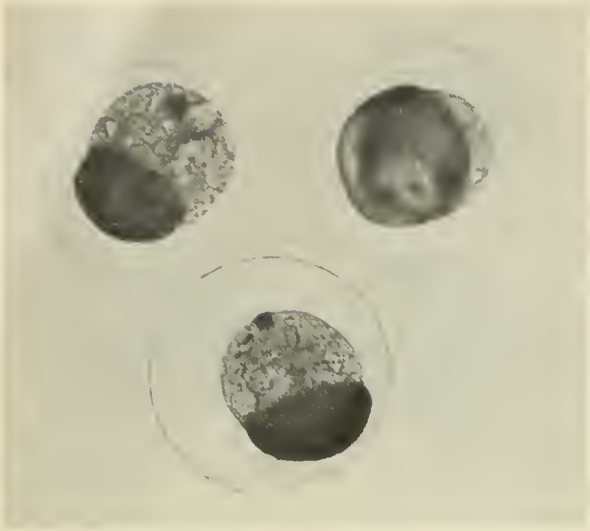

FIGURE 8.—Circa 14-hour stage with blastodermal cap.

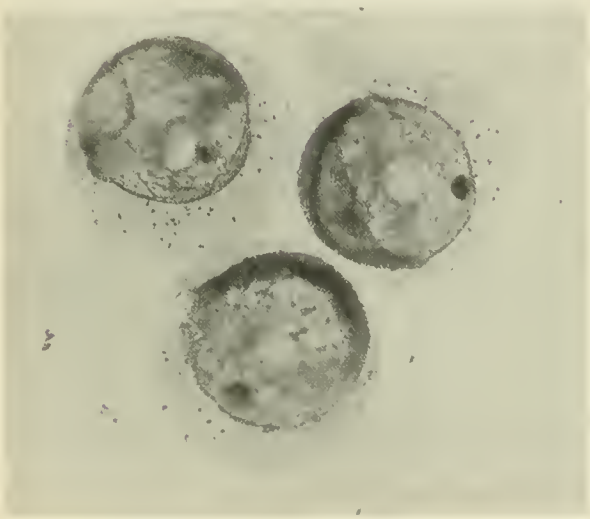

FIGURE 9.—Sixteen-hour stage with embryonic shield.

visible about the time of blastopore closure. Artificially fertilized eggs were not sampled at this stage. Eggs estimated at the 24- and 30-hour stages were obtained from plankton collections made during the rearing studies. Particles adhered to the surface of artificially reared eggs, probably due to the absence of water movement in the culture bowls. Eggs from the plankton were clean by comparison.

The early-stage eggs showed little pigmentation. A few small chromatophores were scattered over the surface of the yolk, but none was apparent on the blastula or early neurula.

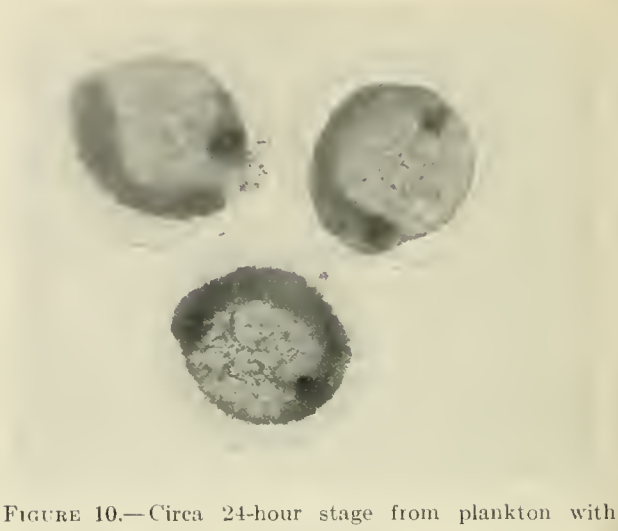

FIGURE 10.—Circa 24-hour stage from plankton with early neurula.

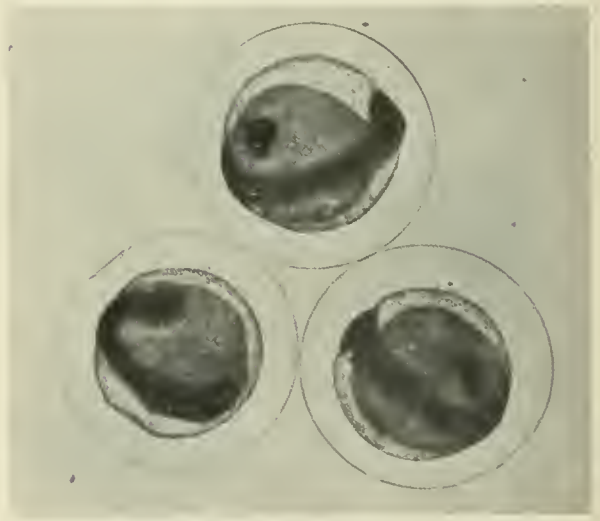

FIGURE 11.—Circa 30-hour stage from plankton with late neurula.

MIDDLE-STAGE EGG

The developing embryo encircled two-thirds of the yolk. Myomeres were visible along most of the embryo, the head was well-defined, and the optic lobes appeared as lateral expansions (fig. 11). The late neurula was raised above the yolk as a cylindrical embryo and not as a mere thickening of the embryonic shield (fig. 12). At the end of this stage, the tail had become separated from the yolk and was curved laterally away from the embryonic axis (fig. 13). This occurred 40 hours after fertilization. Small chromatophores developed on the yolk, and several appeared along the embryo, usually just posterior to the head.

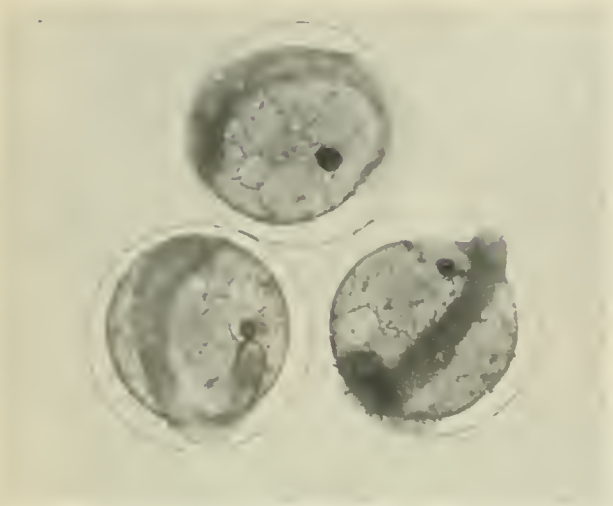

FIGURE 12.—Thirty-eight-hour stage with early embryo.

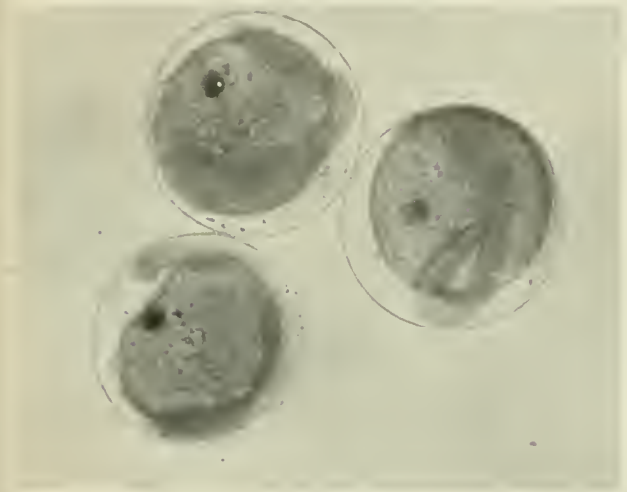

FIGURE 13.—Forty-one-hour stage with tail separating from yolk.

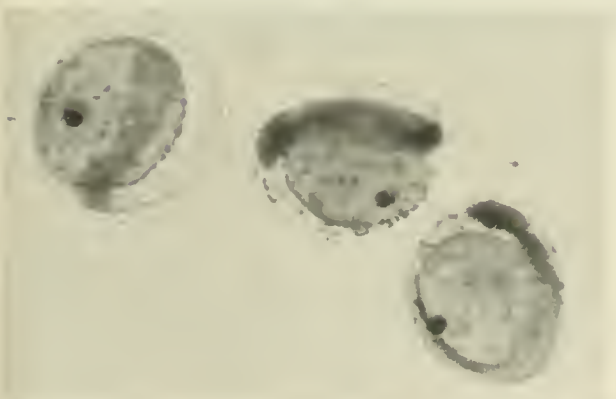

FIGURE 14.—Forty-six-hour stage with late embryo.

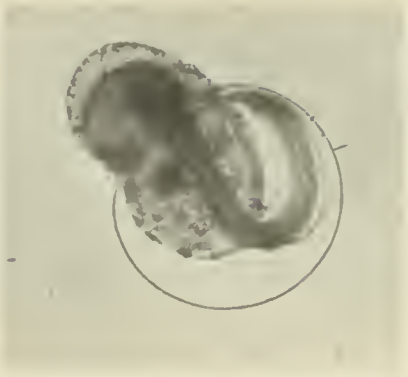

FIGURE 15.—Forty-six-hour stage hatching.

LATE-STAGE EGG

The embryo had grown so large that the tail, free of the yolk, fell just short of touching the head (fig. 14). The somites were visible except near the end of the tail. The embryo was very active, exhibiting convulsive movements at frequent intervals. The tail was outlined with a distinct finfold. Pigmentation generally was limited to one to three small chromatophores along the tail and three to eight in the head or anterior region. Pigmentation of embryos was variable, and no pattern or concentration of chromatophores was discernible. Hatching occurred with the rupture of the external membrane, and the larva emerged, head first (fig. 15), 46 hours after fertilization.

YOLK-SAC LARVA

Yellowfin menhaden, like many other fishes with pelagic eggs (Ahlstrom and Counts, 1955), hatched in a relatively undeveloped condition. The mouth had not formed, and the eyes were unpigmented. Fin rays had not developed, and the pectoral fin buds were not visible. However, the anus had formed and was discernible as a tube passing through the finfold.

The early larva (figs. 16 and 17) floated ventral side up, with the yolk and oil globule uppermost, except during brief, convulsive swimming. During initial swimming, the larva oriented dorsal side up and then, in a head-down position, would move towards the bottom. Body movement would stop after a few seconds and the larva would turn ventral side up and float towards the surface. Such behavior was most marked during the first 24 hours. As the larva grew and the yolk diminished, swimming increased and by 48 hours was

nearly continuous. Even during brief periods of rest, vertical stability was maintained with the dorsal surface up.

Measurements of larvae are given in table 2. The larvae nearly doubled in length during the absorption of the yolk; however, 80 percent of this increase occurred during the first 27 hours.

The late larva continued to lengthen slightly after the 27-hour stage (fig. 18). Between 40 and 60 hours the most apparent change was the shrinking yolk sac (figs. 19 and 20). At the 62-hour stage, eye pigment developed, and the mouth opened (fig. 19). Swimming was continuous and directed as the larva moved across a 6-inch culture bowl with apparent ease. It constantly counteracted the bouyancy of the yolk by swimming in a head-down position. Prior to the development of eye pigment, larvae appeared randomly distributed in the culture bowl and did not react to the approach of the pipette used to collect samples. After the appearance of pigment, larvae oriented away from the source of light and swam from the approaching pipette.

Pigmentation of yolk-sac larvae was limited to widely spaced, small chromatophores along the sides and on the finfold. The chromatophores appeared as faint speckling at a magnification of 20 × and as distinct structures at 100 ×.

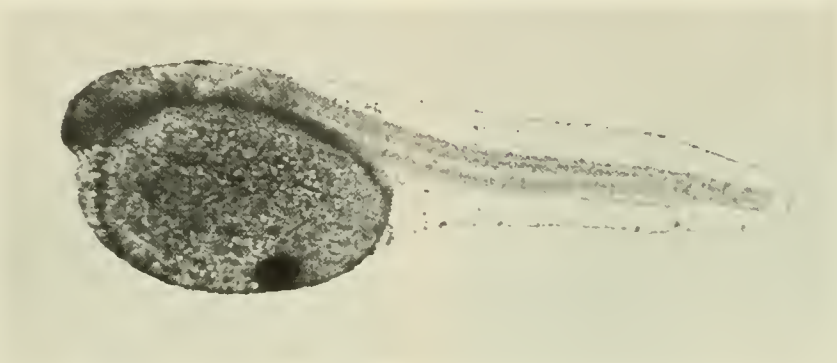

FIGURE 16.—Newly hatched larva 2.8 millimeters long.

FIGURE 17.—Sixteen-hour larva 4.0 mm. long.

TABLE 2.—*Measurements* [1] *of yellowfin menhaden yolk-sac larvae, in millimeters*

(N = 10 specimens at each age)

Hours since hatching	Total length		Distance snout to anus		Yolk-sac length		Yolk-sac width	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
0	2.70–2.92	2.79	2.26–2.42	2.35	1.10–1.21	1.16	0.77–.94	0.83
16	3.85–4.18	4.03	3.24–3.41	3.32	1.10–1.21	1.16	.72–.77	.74
27	4.24–4.68	4.46	3.41–3.68	3.59	.94–1.04	1.00	.66–.72	.67
40	4.34–4.62	4.49	3.46–3.74	3.57	.77– .88	.81	.50–.60	.54
62	4.43–5.28	4.86	3.58–4.18	3.79	.38– .60	.53	.22–.39	.27

[1] Measurements of yolk-sac larvae were of preserved material. Ahlstrom and Ball (1954) estimated as much as 20 percent shrinkage due to formalin preservation. Investigators examining fresh larvae should interpret the measurements accordingly.

FIGURE 18.—Twenty-seven-hour larva 4.5 mm. long.

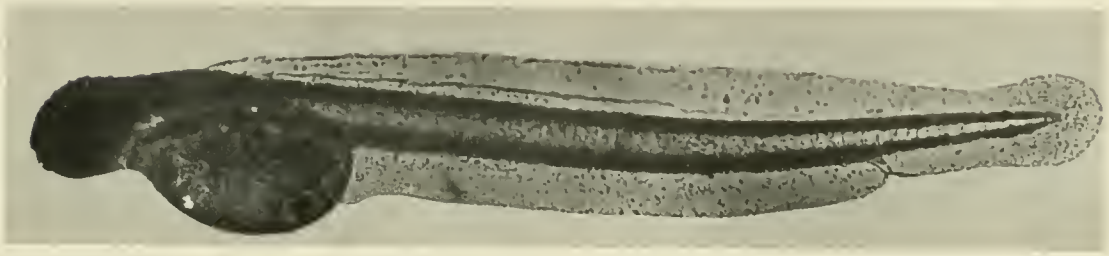

FIGURE 19.—Forty-hour larva 4.5 mm. long.

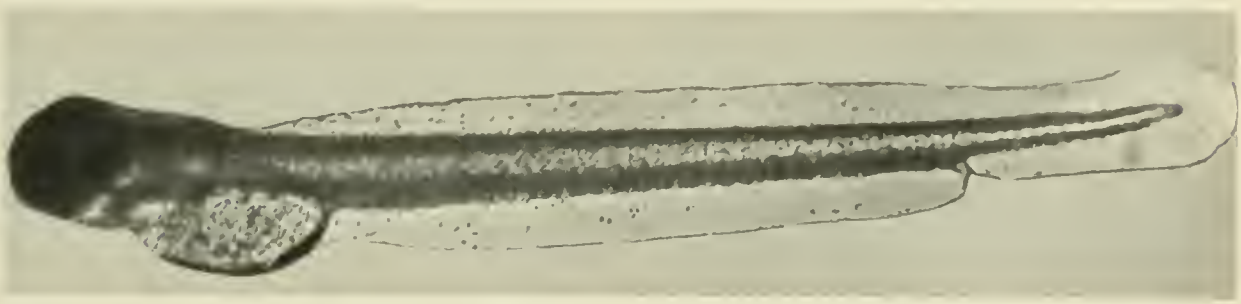

FIGURE 20.—Sixty-two-hour larva 4.9 mm. long.

The rest of the larvae died within a few hours after the 62-hour stage.

I wish to acknowledge the facilities and help furnished by Sembler Fisheries, Sebastian, Fla. Persons connected with the firm gave direct assistance during regular and trial fishing trips, plankton tow-net collections, and examination of the landings.

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DEVELOPMENT AND DISTRIBUTION OF THE SHORT BIGEYE *PSEUDOPRIACANTHUS ALTUS* (GILL), IN THE WESTERN NORTH ATLANTIC

By David K. Caldwell, *Fishery Research Biologist*

Bureau of Commercial Fisheries

The initial phase of a biological inventory of the marine waters between the Florida Straits and Cape Hatteras, N.C., included the collection of both plankton and dip-net samples of larger pelagic organisms during the biological, chemical, and oceanographic operations of the U.S. Fish and Wildlife Service research vessel *Theodore N. Gill*. Nine cruises were conducted to a prearranged network of stations (Anderson, Gehringer, and Cohen, 1956) from January 1953 to December 1954. Part of the second phase of this inventory is the identification of larval and prejuvenile fishes collected at sea. Series of these small fishes provide excellent opportunities for studying phases of the early life histories.

Understanding life histories of fishes, even though all species may not be of direct commercial value, is necessary for an understanding of the interrelationships of different forms and for an intelligent analysis of the biological potential of an area. Such is particularly true when the species under study demonstrates ecological principles which might later be applied to the management of commercial, sport, or forage fishes. *Pseudopriacanthus altus* (Gill), the short bigeye, of the family Priacanthidae, is an example of such a species. A discussion of the distribution and development of this species contributes to a general knowledge of the biology of the fishes of an area which is undergoing extensive study to determine its biological potential and productivity.

This paper, based on collections of the *Theodore N. Gill* and material from other sources, provides a description of the very early development of the short bigeye and carries this development through to the adult stage. The ecological requirements are discussed, along with life history and systematic notes, and geographical distribution. The study provides meristic, morphological, and morphometric characters that form a basis for comparisons with other members of the genus from other geographical areas. Materials are provided which more clearly define generic relationships and solidify family characteristics.

It is appropriate that the operations of the vessel named for the author of this species should, nearly a century later, contribute so materially, in the form of data and specimens, to an understanding of the early life history of the species.

Various staff members of the Bureau of Commercial Fisheries Biological Laboratory at Brunswick, Ga., assisted in gathering and processing data used in this paper. W. I. Follett and Mrs. Lillian Dempster made many constructive suggestions regarding the manuscript; elsewhere in the text, where appropriate, I have mentioned others who were most helpful during the course of the work. In addition, W. B. Gray, of the Miami Seaquarium, provided useful comments on living specimens.

NOMENCLATURE

Pending conclusions from a worldwide revision of this group being prepared by W. I. Follett, of the California Academy of Sciences, and myself, I use the generic name *Pseudopriacanthus* Bleeker instead of *Pristigenys* Agassiz, that is sometimes used. *Pristigenys* was first applied to a fossil fish, and if that form should prove synonymous with the living one, it will have nomenclatorial priority for the species *altus* (and other species of the Pacific). Myers (1958: p. 40) briefly discussed this problem recently, calling attention to an earlier paper (White, 1936: p. 49) on the same subject. Myers (p. 41) pointed out that

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the etymological root of *Pristigenys* is feminine in gender, and if that generic name is accepted the Atlantic short bigeye should be *Pristigenys alta* (Gill).

METHODS

COUNTS

Counts of meristic characters were made under magnification. Aberrant counts were omitted if the apparent result of injury or were verified if the specimen appeared normal otherwise.

MEASUREMENTS

Measurements were made in straight lines between points, never over the curve of the part, and were recorded to the nearest 0.1 mm. Measurements on fish less than about 10 mm. were made with a micrometer eyepiece and a stereomicroscope; those on fish of about 10 to 25 mm. were made with the micrometer eyepiece or a pair of fine-pointed dial calipers (calibrated to tenths of a millimeter) under magnification; and those on larger fish were made with the calipers. Body parts showing injury or damage were not measured.

CONSTRUCTION OF GRAPHS

Arithmetical plots of empirical data were used in graphs of selected body parts in relation to standard length. In addition, eye diameter into standard length was plotted in relation to standard length. Trend lines were not drawn, except in the character of eye diameter, but were determined by visual examination of the plots. The term "inflection," in the discussion of body proportions in relation to size, follows Martin (1949) and denotes a change in slope of the line.

FISH ILLUSTRATIONS

Larvae were illustrated by elaborating detail on ink drawings made at the Brunswick laboratory by Mrs. Fanny Lee Phillips about 1955. The same specimens were used by each of us.

THEODORE N. GILL COLLECTIONS

The larvae and several of the prejuveniles were from collections from *Gill* cruises, and the network of collecting stations is described by Anderson, Gehringer, and Cohen (1956). The abbreviation "Reg." (regular station) in association with the depository prefix BLBG applies to *Gill* cruises and specimens listed in table 1.

DEFINITIONS

MEASUREMENTS

Standard length.—Distance from tip of snout (all measurements involving the snout were at the lateral projection not at the midline) to posterior end of hypural plate (base of midcaudal rays), or tip of urostyle in larvae. Unless otherwise noted, all lengths of specimens referred to are in standard length.

Depth A.—Distance from anterior edge of insertion of pelvic spine to midpoint of base of third dorsal spine.

Depth B.—Distance from midpoint of base of third anal spine to midpoint of base of last dorsal spine.

Head length.—Distance from tip of snout to posterior edge of fleshy part of operculum.

Snout length.—Distance between inner edge of anterior circumorbitals at middle of nostrils and tip of snout.

Postorbital length.—Least distance between inner margins of posterior circumorbitals and posterior edge of fleshy part of operculum.

Eye diameter.—Horizontal diameter from inner margin of anterior circumorbitals at lower level of nostrils to inner margin of posterior circumorbitals.

Interorbital width.—Least distance across top of head between inner margins of dorsal circumorbitals of each eye.

Least depth of caudal peduncle.—Distance on a vertical with midline axis of body.

Dorsal-fin base and anal-fin base.—Distance from anterior edge of base of first spine of fin to posterior edge of base of last segmented ray of fin.

Pectoral-fin length.—Distance from inner dorsal edge of base of most-dorsal element to tip of longest ray with fin laid flat against the body.

Pelvic-spine length, second pelvic soft-ray length, third dorsal soft-ray length, and third anal soft-ray length.—Distance in an erected position on a chord from midpoint of their bases to their tips.

Snout to dorsal-fin origin and snout to anal-fin origin.—Distance from tip of snout to anterior edge of base of first spine in each fin.

Snout to dorsal-fin termination.—Distance from tip of snout to posterior edge of base of last soft-ray of fin.

Snout to pectoral-fin origin.—Distance from tip of snout to inner dorsal edge of base of most-dorsal element of fin.

Pectoral-fin origin to midcaudal base.—Distance from inner dorsal edge of base of most-dorsal element of pectoral fin to base of midcaudal rays.

Dorsal-fin and anal-fin origin to midcaudal base.—Distance from anterior edge of base of first spine of fin to base of midcaudal rays.

Dorsal-fin and anal-fin termination to midcaudal base.—Distance from posterior edge of base of last soft-ray of fin to base of midcaudal rays.

COUNTS

Dorsal and anal spines.—There are ten dorsal and three anal spines, all clearly visible and separate. Numbers are recorded in Roman numerals.

Dorsal and anal soft-rays.—Normally there are 11 dorsal and 10 anal soft-rays. The last soft-ray of each fin, split to the base, was counted as one. As the base of the penultimate soft-ray is often very close to the base of the last split ray, its ray should not be considered the anteriormost branch of a doubly split soft-ray. Numbers are recorded in Arabic numerals.

Pectoral fin.—All rays in both fins were counted, including rudiments. All are segmented, at least in large adults (the most-dorsal segments at a large size), and all but the most-dorsal and the two most-ventral become branched. Numbers are recorded in Arabic numerals.

Pelvic fin.—It has a single spine, similar in structure to spines of the vertical fins, and five soft-rays (one of my specimens had four soft-rays in one fin).

Caudal fin.—The caudal fin has 16 principal rays equally distributed between the two lobes, as is characteristic in the family Priacanthidae. All are segmented, and the innermost 14 are branched. There is also a small number of segmented secondary rays.

Gill rakers.—Counts were made on the first arch, usually on the right side. Rudimentary gill rakers, often one or two occurring at the origin of either limb, were included. A gill raker located at the junction (angle) of the upper and lower limbs was included in the count for the lower limb.

Pored lateral-line scales.—Only scales with a complete tube were counted, usually on the left side of the specimen, from the upper angle of the opercular opening back to and including the scale covering the base of the midcaudal rays. The several additional pored scales extending onto the caudal rays were not counted. Sometimes the tube system extended onto an adjacent scale slightly above or below the main scale, but this incompletely pored scale was not counted. Judgement as to completeness of a tube may distort the scale count by one or two scales. Counts were considered the more accurate on larger specimens.

Vertical scale rows.—The number of anteriorly oblique vertical scale rows was counted along the midline of the body, usually on the left side, beginning at a point just below the anterior terminus of the lateral line (counting from and including the first complete scale on the cleithrum) and continuing posteriorly to the base of the caudal fin. Like the pored-scale row, several vertical rows of scales continue onto the fin, and the last row counted was the one which, when visually extended anterodorsally, included the last pored scale counted (the scale covering the base of the midcaudal rays). Counts of the number of rows on a fish may vary one or two rows due to the sometimes irregular arrangement of the rows, and counts made on larger fish were considered the more reliable.

Scales above and below lateral line.—Scales above the lateral line were counted in an anteriorly directed oblique line to the origin of the dorsal fin, and those below in a posteriorly directed oblique line to the origin of the anal fin. Scales are subject to crowding in the region adjacent to the fins and the counts could not always be made accurately, except on the largest fish. Pored lateral-line scales were not included in a count.

PIGMENTATION

Descriptions of pigmentation represented in the drawings and photographs were made from microscopic observations of preserved individuals. Chromatophores may have faded from some of the smaller specimens, and descriptions of these fish may be incomplete.

DEVELOPMENTAL STAGES

Larval.—Defined as the stage of development beginning with hatching and ending with formation of the adult complement of all fin rays, or in *P. altus* when about 7–8 mm. A ray was considered to be completely formed when it became partially ossified (determined by its staining red

when treated with alizarin). Larvae of this species are pelagic on the open sea.

Prejuvenile.—Defined as beginning with end of the larval stage and continuing until the individual leaves its pelagic habitat, descends to the bottom, and completes a transformation in physical appearance to that of the juvenile and adult. Early prejuveniles have immaculate soft dorsal and anal fins; later ones have the soft parts of the vertical fins spotted, with or without a black edge. The maximum size for prejuveniles in nature apparently is about 65 mm.

Juvenile.—Defined as commencing when transformation to the adult physical appearance is complete (in the bottom habitat) and terminating with attainment of sexual maturity. In both juveniles and adults the soft parts of the vertical fins are immaculate except for a black edge. The size at which the juvenile-adult transition stage is reached was not determined.

Adult.—Defined as starting with the onset of sexual maturity.

STUDY MATERIAL

The larvae of *P. altus* used in this study were collected during plankton surveys conducted from the M/V *Theodore N. Gill* in the waters off the Atlantic coast of the southeastern United States by the U.S. Fish and Wildlife Service South Atlantic Fishery Investigations (now Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia). Several prejuvenile and numerous adult specimens are also deposited at this laboratory as a result of exploratory-fishing operations conducted by other Bureau vessels (primarily M/V *Oregon, Silver Bay,* and *Combat*) and my own collections. All of the material at this laboratory is referred to in this paper by the letters BLBG (no catalog numbers) and accompanying pertinent data.

This study material was greatly supplemented, especially in the middle sizes, by specimens from various institutions. I am most grateful to the persons named here for permitting me to examine materials in their charge or, in two instances, for examining specimens for me. These persons and their institutions, collections, or the place in which they examined specimens include—

United States National Museum (USNM), through Leonard P. Schultz; Chicago Natural History Museum (CNHM), through Loren P. Woods; Academy of Natural Sciences of Philadelphia (ANSP), through James E. Böhlke; Woods Hole Oceanographic Institution (WHOI), through Richard H. Backus; University of Florida Collections (UF), through John C. Briggs, John D. Kilby, and Daniel M. Cohen; Bingham Oceanographic Collection (BOC), through James E. Morrow; Tulane University (TU), through Royal D. Suttkus; University of Georgia (UG), through Donald C. Scott; Charleston Museum (ChM), through E. Milby Burton; University of Miami Ichthyological Museum (UMIM), through Luis R. Rivas; University of North Carolina Institute of Fisheries (UNC), through Earl E. Deubler; Stanford University Natural History Museum (SU), through George S. Myers and the late Margaret Storey; University of Miami Marine Laboratory (UMML), through C. Richard Robins; Cornell University (CU), through Edward C. Raney; California Academy of Sciences (CAS), which includes old Indiana University numbers (IUM), through W. I. Follett; U.S. Fish and Wildlife Service Ichthyological Laboratory, U.S. National Museum (USFWS Ich. Lab.), through Giles W. Mead; M/V *Delaware* collections, through Robert H. Gibbs (RHG); Academy of Sciences in Havana, Cuba (ASH), examined by P. P. Duarte Bello and Jose Suárez Caabro; Museum of the Naval Academy at Mariel, Cuba (MNAMC), examined by Duarte Bello and Suárez Caabro. In addition to these, I am particularly grateful to Winfield Brady, who is now, and J. B. Siebenaler, who was then, of Florida's Gulfarium, Fort Walton Beach; to F. G. Wood of Marine Studios, Marineland, Florida; and to Craig Phillips, who was then of the Miami Seaquarium, for specimens deposited for this study at this laboratory and at the University of Florida Collections.

Specimens examined and their present location are listed in table 1. Where available, data as to depth of capture for bottom-caught individuals and, in pelagic specimens, depth of water over which capture was made, are also included. Estimated depths are from hydrographic charts. Habitats are listed with question marks when data with the specimen were incomplete—the habitat being inferred either from the geographical location or physical appearance of the specimen as compared with that of specimens of known habitat.

TABLE 1.—*Location and date of capture, number, size range, habitat, metamorphic stage, and present location of 264 specimens of* Pseudopriacanthus altus *studied*

[Metamorphic stages, based on vertical fin coloration: Pretransformation (P), transforming (T), completely transformed (C)]

Location	Date captured	Number of specimens	Size (mm.)	Collection [1]	Habitat [2]	Metamorphic stage
ATLANTIC OCEAN:						
Massachusetts	No date	2	49.3–57.1	CNHM 55986	Pelagic (?)	T, P
Katama Bay, Mass	Aug. 30, 1899	1	41.1	USNM 49665	do	P
Do	do	1	48.2	USNM 49618	do	P
Do	Sept. 1, 1899	6	30.8–47.3	USNM 49664	do	P, T
Do	Sept. 16, 1899	1	49.0	USNM 126831	do	P
Do	do	1	(?)	CAS 20584 (IUM 9323)	do	
Do	Sept. 19, 1899	1	47.1	USNM 63928	do	P
Do	1900	4	34.5–55.9	USNM 68129	do	P, T
Do	No date	1	53.9	CNHM 7690	do	P
Do	do	8	27.9–45.6	USNM 58892	do	P
Do	do	22	26.4–52.0	USNM 58831	do	P
Woods Hole, Mass	Sept. 29, 1875	1	44.2	USNM 15583	do	P
Do	Sept. 26, 1877	1	32.8	USNM 20642	do	P
Do	October 1899	1	37.1	USNM 58832	do	P
Do	do	2	35.7–41.1	USNM 58833	do	T, P
Do	do	1	57.3	USNM 85780	do	T
Acushnet River, Mass	Nov. 1, 1890	3	25.6–53.5	USNM 43732	do	
Newport, R.I.	No date	1	(?)	CAS 20583 (IUM 8919)	do	
Rhode Island	October 1875	1	23.5	USNM 37377	do	P
Outside New Haven Harbor, Conn.	Oct. 8, 1956	1	36.4	BOC 3738	Bottom, 3.3 fathoms	P
Fire Island Inlet, Long Island, N.Y.	Aug. 11, 1938	2	33.9–34.0	CU 27831	Pelagic (?)	P
Do	do	1	33.2	CU 33112	do	P
Long Beach, Long Island, N.Y.	No date	1	26.1	ANSP 40220	do	P
Quoque, Long Island, N.Y.	August 1952	2	22.9–24.2	CU 21482	do	P
Tomkinsville, N.Y.	No date	1	52.3	USNM 10763	do	T
39°37′ N., 70°58′ W. to 39°34′ N., 70°54′ W.	Aug. 19–20, 1953	24	12.4–19.9	WHOI, *Blue Dolphin*	Pelagic, ca. 1,300 fathoms	P
Atlantic City, N.J.	No date	1	57.9	ANSP 13315	Pelagic (?)	T
Ventnor, N.J.	Aug. 29, 1931	1	23.2	ANSP 54634	do	P
Do	August–September 1931.	13	21.1–26.6	ANSP 54620–32	do	P
Lovelady Island, N.J.	July 30, 1931	1	27.4	ANSP 54633	do	P
Corson Inlet, N.J.	Sept. 17, 1928	1	38.8	ANSP 51398	do	P
39°07′ N., 65°58′ W.	Sept. 21, 1957	1	10.2	RHG, *Delaware*	Pelagic, ca. 2,500 fathoms	P
38°37′ N., 68°14′ W.	July 13, 1958	3	11.3–13.9	do	Pelagic, ca. 2,000 fathoms	P
38°25′ N., 72°40′ W.	1885	1	19.9	USNM 155627, *Albatross*	Pelagic (?)	P
38°10′ N., 68°10′ W.	June 11, 1957	1	13.8	WHOI, *Delaware*	Pelagic, ca. 2,320 fathoms	P
Off Ocean View, Va.	Sept. 26, 1922	1	54.3	USNM 155612	Pelagic	T
34°55′ N., 75°31′ W. to 34°55.5′ N., 75°32′ W.	June (?) 3, 1885	1	196.9	USNM 151917, *Albatross*	Bottom, ca. 25 fathoms	C
34°46′ N., 76°23′ W.	Sept. 10, 1959	1	44.4	BLBG, *Silver Bay* 1263	Bottom, 4–6 fathoms	P
34°46′ N., 76°04′ W.	Sept. 12, 1959	1	62.5	BLBG, *Silver Bay* 1273	Bottom, 17 fathoms	T
34°38′ N., 76°49′ W.	Sept. 22, 1959	1	42.9	BLBG, *Silver Bay* 1291	Bottom, 8–10 fathoms	P
34°36′ N., 75°53′ W.	Aug. 12, 1953	3	3.2–3.9	BLBG, *Gill* Cr. 3, reg. 75	Pelagic, 22 fathoms	P
Ca. 34°35′ N., 75°52′ W.	Oct. 18, 1885	1	16.1	USNM 83884, *Albatross* (sta. 2606?).	Pelagic, ca. 25 fathoms	P
34°32′ N., 75°53′ W.	Sept. 11, 1959	1	58.9	BLBG, *Silver Bay* 1268	Bottom, 30–31 fathoms	T
18 mi. SW of Cape Lookout, N.C.	Feb. 8, 1956	1	225.4	UNC 132, *William J.*	Bottom, 50 fathoms	C
Off Cape Lookout, N.C.	Sept. 2, 1914	1	3.4	USNM 111796, *Albatross*	Pelagic	P
Off Cape Lookout Light Ship, N.C.	do	2	5.2–5.8	USNM 111795, *Fish Hawk*	do	P
34°21′ N., 76°34′ W.	Sept. 23, 1959	2	48.6–49.4	BLBG, *Silver Bay* 1299	Bottom, 14 fathoms	T, P
34°09′ N., 76°02′ W.	Oct. 19, 1885	2	10.5–11.2	USNM 111797, *Albatross*	Pelagic, ca. 250 fathoms	P
33°57′ N., 77°01′ W.	Sept. 4, 1959	1	15.0	BLBG, *Silver Bay* 1222	Pelagic, 16–17 fathoms	P
33°44′ N., 77°00′ W.	Aug. 11, 1953	2	2.6–2.7	BLBG, *Gill* Cr. 3, reg. 65	Pelagic, 21 fathoms	P
33°40.5′ N., 76°59.5′ W.	Dec. 9, 1959	1	213.2	BLBG, *Silver Bay* 1506	Bottom, 21–22 fathoms	C
33°39′ N., 76°48′ W.	do	5	86.2–208.6	BLBG, *Silver Bay* 1505	Bottom, 55–58 fathoms	C
33°35′ N., 76°50′ W.	June 16, 1957	1	210.7	UNC 1324, *La Gatita*	Bottom, 37.5 fathoms	C
33°29′ N., 76°40′ W.	Aug. 11, 1953	1	2.7	BLBG, *Gill* Cr. 3, reg. 64	Pelagic, 210 fathoms	P
33°11′ N., 77°31′ W.	Feb. 27, 1960	1	ca. 250	BLBG, *Silver Bay* 1672	Bottom, 30–32 fathoms	C
33°04′ N., 77°59′ W.	Mar. 7, 1960	2	90.5–133.4	BLBG, *Silver Bay* 1738	Bottom, 20–21 fathoms	C
33°03′ N., 78°21′ W.	Sept. 26, 1954	1	15.0	BLBG, *Gill* Cr. 8, reg. 54	Pelagic, 17 fathoms	P
Off Cape Romain, S.C.	Jan. 5, 1937	1	166.5	ChM 37.3.6, *Richard and Arnold.*	Bottom, 20 fathoms	C
32°51′ N., 78°32′ W.	Oct. 20, 1959	1	179.3	BLBG, *Silver Bay* 1360	Bottom, 19–21 fathoms	C
32°58′ N., 78°15′ W.	Sept. 26, 1954	1	ca. 15	BLBG, *Gill* Cr. 8, reg. 53–54	Pelagic(?) [3]	
32°40′ N., 76°46′ W.	July 6, 1954	2	8.6–8.7	BLBG, *Gill* Cr. 7, reg. 62	Pelagic, 445 fathoms	P
32°37′ N., 78°49′ W.	Mar. 8, 1960	1	103.1	BLBG, *Silver Bay* 1743	Bottom, 18–21 fathoms	C
32°32′ N., 78°40′ W.	Oct. 26, 1959	32	161.0–261.8	BLBG, *Silver Bay* 1393	Bottom, 40–50 fathoms	C
32°32′ N., 79°01′ W.	June 25, 1957	1	79.5	UMIM 1985, *Combat* 427	Bottom, 35 fathoms	
32°12′ N., 78°26′ W.	Aug. 9, 1953	2	4.4–6.6	BLBG, *Gill* Cr. 3, reg. 49	Pelagic, 190 fathoms	P
31°57′ N., 79°16′ W.	Aug. 6, 1953	1	8.3	BLBG, *Gill* Cr. 3, reg. 42	Pelagic, 72 fathoms	P
31°36′ N., 79°52′ W.	July 2, 1954	1	12.1	BLBG, *Gill* Cr. 7, reg. 38	Pelagic, 27 fathoms	P
31°35′ N., 79°51′ W.	Aug. 5, 1953	2	2.4–5.3	BLBG, *Gill* Cr. 3, reg. 38	Pelagic, 25 fathoms	P
Charleston, S.C.	No date	1	227.0	SU 10409	Bottom	C
18 mi. SE. of Charleston, S.C.	Apr. 4, 1939	1	167.5	ChM 50.136.32, *Holokai*	Bottom, ca. 7 fathoms	C
Off Charleston, S.C.	Oct. 9, 1931	1	215.6	ChM 31.237.3	Bottom	C
Commercial trawling area, Brunswick, Ga.	Sept. 18–19, 1956	1	24.1	BLBG	Bottom, ca. 3 fathoms	P
31°02′ N., 80°00′ W.	July 30, 1953	2	4.8–8.2	BLBG, *Gill* Cr. 3, reg. 31	Pelagic, 29 fathoms	P
30°11′ N., 80°17′ W.	Aug. 31, 1956	1	84.5	USFWS Ich. Lab., *Combat* 72.	Bottom, 32 fathoms	C
30°01′ N., 80°32′ W.	Jan. 14, 1957	1	92.7	USFWS Ich. Lab., *Combat* 203.	Bottom, 22 fathoms	C
Off St. Augustine, Fla.	Oct. 3, 1956	1	47.2	BLBG	Bottom, ca. 10 fathoms	T

See footnotes at end of table.

TABLE 1.—*Location and date of capture, number, size range, habitat, metamorphic stage, and present location of 264 specimens of* Pseudopriacanthus altus *studied*—Continued

[Metamorphic stages, based on vertical fin coloration: Pretransformation (P), transforming (T), completely transformed (C)]

Location	Date captured	Number of specimens	Size (mm.)	Collection [1]	Habitat [2]	Metamorphic stage
ATLANTIC OCEAN—Continued						
29°43′ N., 80°25′ W.	May 4, 1960	1	129.8	BLBG, *Silver Bay* 2079	Bottom, 20–22 fathoms	C
29°40′ N., 80°22′ W.	July 28, 1953	1	4.0	BLBG, *Gill* Cr. 3, reg. 19	Pelagic, 25 fathoms	P
29°00′ N., 80°11′ W.	July 27, 1953	1	Head only	BLBG, *Gill* Cr. 3, reg. 14	Pelagic, 36 fathoms	
28°21′ N., 80°09′ W.	Sept. 12, 1954	1	3.5	BLBG, *Gill* Cr. 8, reg. 10	Pelagic, 23 fathoms	P
27°00′ N., 79°18′ W.	July 25, 1953	1	2.2	BLBG, *Gill* Cr. 3, reg. 1	Pelagic, 370 fathoms	P
Off W. tip Grand Bahama Island.	Oct. 3, 1953	1	Ca. 19	BLBG, *Gill* Cr. 4	Pelagic (?) [4]	
26°31′ N., 80°01′ W.	Mar. 25, 1956	2	59.0–72.0	UMIM 1191, *Pelican* 15	Bottom, 30–35 fathoms	
Baker's Haulover, Miami Beach, Fla.	Nov. 28, 1955	1	137.2	UMIM 1847	Bottom	C
Near Cutler, Biscayne Bay, Fla.	July 26, 1958	1	43.5	BLBG	do	T
Soldier Key, near Miami, Fla.	Ca. August 1954	1	73.2	do	Bottom, 3 fathoms	T
25°10′ N., 80°02′ W.	Sept. 22, 1957	1	16.9	BLBG, *Combat* 438	Pelagic, 200 fathoms	P
Bermuda	1911	1	23.8	CNHM 48584	Pelagic(?)	P
"Bermuda?"	No date	1	236.0	CNHM 48608	Bottom(?)	C
GULF OF MEXICO:						
Deadman's Bay, Fla.	do	1	37.6	USNM 73063, *Fish Hawk*	do	P
24°25′ N., 81°46′ W.	1885 (Jan. 15?)	1	96.3	USNM 37772, *Albatross*	Bottom, ca. 75 fathoms	C
Do.	Jan. 15, 1885	4	63.2–106.0	USNM 84498, *Albatross*	do	C
24°25′ N., 81°47′ W.	do	1	66.1	USNM 134165, *Albatross*	Bottom(?), ca. 75 fathoms	C
Dry Tortugas, Fla.	No date	1	39.9	USNM 117086	Bottom(?)	P
10 mi. N. of Loggerhead Key, Dry Tortugas, Fla.	Sept. 26, 1958	1	50.5	UMIM 2370	Bottom, ca. 20 fathoms	
20 mi. NE. of Dry Tortugas, Fla.	March 1950	1	92.4	UMIM 209	Bottom, ca. 18 fathoms	C
25 mi. NNE. of Dry Tortugas, Fla.	Mar. 1–6, 1950	2	87.2–94.3	UG 161	Bottom, 17–18 fathoms	C
30 mi. NE. of Loggerhead Key, Dry Tortugas, Fla.	No date	2	67.3–77.9	UF 1434	Bottom	C
24°59′ N., 83°35′ W.	Apr. 19, 1954	1	65.2	CNHM 59894, *Oregon* 1022	Bottom, 39 fathoms	T
Do.	do	2	78.2–90.4	USFWS Ich. Lab., *Oregon* 1022.	do	C
Do.	do	1	70.8	TU 13201, *Oregon* 1022	do	C
Lemon City, Fla.	No date	1	47.2	USNM 181345	Bottom(?)	P
27°07′ N., 83°19′ W.	Apr. 4, 1954	1	45.2	CNHM 59893, *Oregon* 963	Bottom, 23 fathoms	T
27°36′ N., 83°41′ W.	Jan. 27, 1951	1	92.1	TU 2694, *Oregon* 255	Bottom, 25 fathoms	C
Anclotte Key, Pasco County, Fla.	August 1929	1	204.3	UF 4214	Bottom(?)	C
28°47′ N., 84°37′ W.	Mar. 15, 1885	1	63.4	USNM 84511	Bottom(?), ca. 24 fathoms	T
Do.	Nov. 15, 1885	1	63.7	USNM 132201, *Albatross*	Bottom, ca. 24 fathoms	C
28°50.8′ N., 85°28′ W.	Dec. 17, 1952	1	106.1	CNHM 45488, *Oregon* 732	Bottom, 57 fathoms	C
28°56.5′ N., 85°18′ W.	Dec. 16, 1952	1	79.2	CNHM 45486, *Oregon* 731	Bottom, 40 fathoms	C
29°21′ N., 84°49′ W.	July 26, 1958	1	82.7	BLBG, *Silver Bay* 587	Bottom, 15 fathoms	C
Ca. 25 mi. SW. of Panama City, Fla.	Apr. 19, 1958	1	196.5	BLBG	Bottom, ca. 20 fathoms	C
Inlet at Destin, Fla.	November 1955	1	149.2	UF 5582	Bottom, 2.5 fathoms	C
Ca. 1 mi. off Destin, Fla.	Mar. 30, 1956	1	165.8	UF 5593	Bottom, 16 fathoms	C
Off Destin, Fla.	No date	1	183.6	UF 3950	do	C
Do.	Ca. June 1958	1	201.7	BLBG	do	C
Near Destin, Fla.	Summer 1958	1	176.9	do	Bottom, 17 fathoms	C
Fort Walton Beach, Fla.	August 1958	2	23.3–40.7	do	Bottom, ca. 1 fathom	P
[Off] Pensacola, Fla.	No date	1	161.1	SU 2800	Bottom	C
Pensacola, Fla.	do	2		CAS 20585 (HUM 8570)	Unknown	
30°17′ N., 87°13′ W.	Jan. 23, 1957	1	167.0	CNHM 64180, *Oregon* 1647	Bottom, 7 fathoms	C
12 mi. SSW. of Horn Island, Miss.	Nov. 3, 1931	1	52.6	USNM 155625	Bottom, ca. 10 fathoms	T
28°08′ N., 94°35′ W.	June 29, 1957	1	169.9	TU 16282, *Silver Bay* 10	Bottom, 31 fathoms	C
Within 50 mi. of Corpus Christi, Tex.	1920–40	1	24.0	CNHM 40326	Unknown	
19°48′ N., 91°20′ W.	Aug. 25, 1951	1	40.9	CNHM 46507, *Oregon* 440–445.	Bottom, 14 fathoms	P
20°20′ N., 91°28′ W.	Dec. 11, 1952	1	55.6	UMIM 1848, *Oregon* 721	Bottom, 17 fathoms	T
22°15′ N., 88°55′ W.	Dec. 13, 1952	1	46.6	CNHM 45487, *Oregon* 725	Bottom, 25 fathoms	P
22°32′ N., 88°47′ W.	Jan. 11, 1951	1	71.7	CNHM 46506, *Oregon* 222	Bottom, 29 fathoms	C
WEST INDIES:						
Vedado (Havana), Cuba.	1944	1	Ca. 260	MNAMC (mounted)	Bottom	C
"Cuba"	No date	1	Ca. 250	ASH (mounted)	Unknown	C
18°37.5′ N., 64°57′ W.	Sept. 26, 1959	1	108.3	BLBG, *Oregon* 2608	Bottom, 42 fathoms	C

[1] Collections listed in text, p. 104.
[2] Depths and questioned habitats discussed in text.
[3] Stomach contents: *Euthynnus alletteratus* (Rafinesque).
[4] Stomach contents: *Thunnus atlanticus* (Lesson).

TABLE 2.—*Reliable records of 7* Pseudopriacanthus altus *which were not studied*

[Collected by M/V *Oregon;* first 2 specimens listed by Springer and Bullis (1956: p. 80)]

Station	Locality	Date	Depth (fathoms)
263	29°22′ N., 88°06′ W.	Feb. 16, 1951	45
531	28°25.5′ N., 92°33.5′ W.	Apr. 10, 1952	29
1639	29°49′ N., 87°19′ W.	Jan. 10, 1957	30
1705	29°57′ N., 86°13′ W.	Feb. 12, 1957	25
1786	28°05′ N., 94°54′ W.	Mar. 13, 1957	31
1789	28°07′ N., 95°03′ W.	Mar. 14, 1957	31
1790	28°06′ N., 95°08′ W.	Mar. 14, 1957	31

A few records based on apparently reliable sight identifications of trawled or dredged bottom forms are included in table 2.

GEOGRAPHICAL DISTRIBUTION

Pseudopriacanthus altus has been considered by most authors to be a West Indian species that regularly occurs north to South Carolina on the Atlantic shores of the United States, and to Pensacola, Florida, in the northeastern Gulf of

Mexico (Breder, 1948: p. 168; Bigelow and Schroeder, 1953: p. 410; Boulenger, 1895: p. 359; Hildebrand and Schroeder, 1928: p. 255; Jordan and Evermann, 1896: p. 1240; Jordan, Evermann, and Clark, 1930: p. 323; and Smith, 1907: p. 285). They further noted that this species is found as a straggler in the Gulf Stream as far north as Massachusetts.

Based on available material, recent field work, and the literature, the geographical range of the short bigeye can be stated as extending from Southport, Me. (Scattergood and Coffin, 1957: p. 156), to Horn Island, Mississippi, and scattered localities in the western and southern parts of the Gulf of Mexico (table 1 and fig. 1). It is also known from Bermuda (Beebe and Tee-Van, 1933: p. 141), Cuba (Fowler, 1942b: p. 75; Duarte Bello, 1959: p. 71), and from the vicinity of the Virgin Islands (*Oregon* station 2608). This distribution is similar to that given by Briggs (1958: p. 275), with ecological restrictions to be discussed later.

It is difficult to explain why the short bigeye has almost always been considered a West Indian species, except that early published and perhaps erroneous ranges for fishes from poorly known areas are often copied blindly without reference to faunal studies for specific localities. Evidence for the apparent rareness of *P. altus* in the West Indies, the Caribbean, and from northeastern South America (where the fishes are often very similar to those of the West Indies and the Caribbean) is found in a number of faunal lists which cover these areas and which fail to include the short bigeye. Some of these are Evermann and Marsh, 1902 (Puerto Rico); Cockerell, 1892 (Jamaica); Metzelaar, 1919 (Dutch West Indies), 1922 (Lesser Antilles); Meek and Hildebrand, 1925 (Panama); Bean, 1890 (Cozumel, Yucatan); Fowler, 1919 (Panama, Brazil, Surinam, St. Martin, St. Croix, St. Christopher, Jamaica, Haiti, Bahamas), 1928 (Bahamas, Haiti, Puerto Rico, St. Lucia, Dominica), 1937 (Haiti), 1941 (Brazil), 1944 (numerous Antillean islands and banks, Central America, Cayman Islands), 1951 (Brazil, Patagonia), 1952 (Hispaniola), 1953 (Colombia); Beebe and Tee-Van, 1928 (Haiti, Santo Domingo), 1935 (Haiti, Santo Domingo); Nichols, 1929 (Puerto Rico, Virgin Islands); Herre, 1942 (Antigua, Barbados); Beebe and Hollister, 1935 (Grenadines); Schultz, 1949 (Venezuela); Erdman, 1956 (Puerto Rico); Cope, 1871 (St. Martin, St. Croix, St. Christopher, New Providence); Puyo, 1949 (French Guiana); Miranda-Ribeiro, 1915 (Brazil); Nichols, 1912 (Cuba), 1921 (Turks Island); and Parr, 1930 (Bahamas, Turks Island).

Recent trawling operations by the U.S. Fish and Wildlife Service M/V *Oregon* in the West Indies (where hauls were made over rough bottom which is good habitat for *P. altus*) yielded but one specimen, and extensive trawling off the northeastern coast of South America yielded none.

The species is often taken by handline and in traps in the waters of Florida and the two Carolinas, and both of these methods are and have long been regular forms of commercial fishing throughout the West Indies (often conducted in deep water around rocks—where the species occurs in the United States). Markets where all species so caught are sold also have long been a regular source of specimens for ichthyologists in the West Indies. My own collections in the field and in the markets of Nassau, Havana, and Jamaica have failed to produce *P. altus*. Thus, *P. altus* either must be rare in the West Indies or must occupy a habitat which makes it extremely difficult to collect.

I doubted the presence of *P. altus* in the West Indies—on the lack of records as previously noted—until I enlisted the help of Dr. P. P. Duarte Bello and Dr. Jose Suárez Caabro of the Laboratorio de Biologia Marina of the Universidad Catolica de Santo Tomas de Villanueva at Havana, and until the recent collection of a single specimen by the *Oregon* (station 2608) off the Virgin Islands (table 1). Poey (1856–58, 1866, 1868) did not list this species for Cuba, and it was not until 1875 (p. 114) that he listed a 52-mm. fish as "*Priacanthus*?" and stated that it was like *P. altus* except for color. His specimen could not be located to clarify this record. Fowler listed the species in the collections of the Academy of Sciences in Havana (1942b: p. 75) and a specimen (presumably mounted) at the Instituto de Matanzas (1942a: p. 65). In August 1958, Dr. Duarte Bello told me that the specimen at the Academy of Sciences was actually *P. altus*, though labeled *Pempheris mulleri* Poey, and was approximately 250 mm. in standard length (mounted). The label read only "Cuba." He and Dr. Suárez Caabro found a second mounted specimen, 260 mm. standard length, in the museum of the Naval

FIGURE 1.—Geographical distribution of *Pseudopriacanthus altus*.

Academy in Mariel, Pinar del Rio Province. The example was labeled as having been taken about 1944 at Vedado (Havana), and their conversation with the former curator of that museum confirmed the locality and included the fact that the specimen came from deep waters, "maybe more than 60 fathoms." The data which Duarte Bello sent me from these specimens substantiate his determinations. The following records were received in a later letter from Dr. Duarte Bello, dated September 19, 1960. I have not seen his specimens, which were being maintained alive in the Cuban National Aquarium, but presume his identifications are correct as he is familiar with

the species. The records further substantiate a permanent Cuban population of *P. altus*—at least in the Havana region. The two additional captures are a 134-mm. individual from Jaimanitas, Mariano, La Habana, taken with hook-and-line using squirrelfish as bait on June 18, 1960, in 110 fathoms; and a 196-mm. specimen taken in the same manner at the same depth and locality on August 8, 1960, with grunt as bait.

Duarte Bello (1959: p. 71) listed this species from Vedado (presumably the 260-mm. specimen) and cited Jordan and Evermann (1896: p. 1239) and Jordan, Evermann, and Clark (1930: p. 323) for a Cuban distribution. Larger fishes in collections from the Havana region usually must be questioned as to locality of capture, especially when they are old or when no data other than "Havana" or "Cuba" are given. They may have come from the market, and market fishes sold in Havana were often collected in Florida or Yucatan waters (see Caldwell, 1957: p. 97) which is within the known range of *P. altus*. In view of the findings by Duarte Bello and Suárez Caabro, at least one of the mounted Cuban specimens and the two living individuals must be viewed as adults having valid locality data, and a permanent population may occur there.

With the Cuban and Virgin Islands records, there can be no doubt that *P. altus* occurs, at least occasionally, in the West Indies. An examination of general current systems as outlined by Sverdrup, Johnson, and Fleming (1942: chart VII), Galtsoff (1954: p. 29), and Leipper (1954: p. 121–122) shows that apparently no countercurrents originate in continental waters north of the Caribbean or in Bermuda waters and flow to the Bahamas, Antilles, or the Caribbean in general, that could carry larval *P. altus* to these areas from the north. The Virgin Islands specimen is 108 mm. in length, and presumably nearly adult. The Virgin Islands and Cuban populations of adults undoubtedly contribute to the Gulf Stream (Florida Current) population of larvae and prejuveniles as that current flows through the Straits of Florida. A 19-mm. prejuvenile taken from the stomach of a *Thunnus atlanticus* (Lesson) collected in the vicinity of the western tip of Grand Bahama Island (*Gill* cruise 4, table 1) might have been captured along the eastern edge of the current flowing by Grand Bahama. This bigeye almost certainly came from the Bahamas, Cuba, or the Antilles, as it is unlikely that so small a specimen spawned in the Gulf of Mexico or in Atlantic waters of southern Florida could have made its way across the Gulf Stream. A 2.2-mm. larva was captured in a plankton net at regular station 1 on *Gill* cruise 3 on the eastern side of the Gulf Stream. Presumably the specimen, though probably just hatched, rode the fast flow of the Stream to this point from somewhere in the Bahamas or northern Antilles.

If the West Indian population of adults extends much to the south of the Virgin Islands, its larvae might be expected to the eastward of the Bahamas as well, as certain portions of the North Equatorial Current flow from the Lesser Antilles up along the outside (east) of the Bahamas.

It is likely that the Bermuda population was based originally, and is perhaps in part maintained, on recruitment from the continent or from the West Indies, via branches of the Gulf Stream (see Sverdrup, Johnson, and Fleming (1942: chart VII).

ECOLOGICAL DISTRIBUTION

FACTORS INFLUENCING DISTRIBUTION

Pseudopriacanthus altus may occupy two separate habitats, depending on its stage of development. The larvae and prejuveniles up to approximately 60 mm. standard length are pelagic or have just left this niche, and these stages frequently are taken offshore by dip-net and in plankton or other surface-fishing nets. With one exception, possibly based on adults (a comment by Fowler, 1940: p. 13, that the species was taken in the fall by trawlers working off Cape May, N.J.), all of the specimens that I have seen, and inferences in the literature for others, indicate that *P. altus* is a straggler, through the medium of the Gulf Stream, north of about Cape Hatteras, N.C. I found no large specimens from north of that point in museums, although very small specimens were quite numerous. In continental waters south of Cape Hatteras and in the Gulf of Mexico, large adults were taken by U.S. Fish and Wildlife Service explorations and sport-fishing and commercial boats of various kinds. Large specimens also were seen in museums. Larvae and prejuveniles from southern waters also were collected or were seen in museums.

Larvae are found at or near the surface in or near the edge of the Gulf Stream (fig. 6), which undoubtedly influences their distribution.

Many small specimens, approximately 23 to 58 mm., from the coasts of New Jersey, Long Island (N.Y.), and from the south shores of the Cape Cod region were examined (table 1). As their appearance resembled that of offshore-caught specimens (and from partial data provided with some), it was presumed that these specimens actually were stragglers washed inshore from and by the northward-flowing currents. In fact, *P. altus* was originally described from a 1.2-inch specimen which, according to the author (Gill, 1862: p. 133), probably arrived in Narragansett Bay, R.I., the type locality, via the Gulf Stream. Recently, Scattergood and Coffin (1957: p. 156) and Morrow (1957: p. 241) noted small specimens taken under conditions which indicated that they were settling to the bottom (the one record in a trap set at 10 fathoms, the other in an oyster dredge in 3.3 fathoms). As no adults have been recorded from these waters, it is presumed that these specimens, too, would not have survived. I have examined Morrow's specimen (BOC 3738, table 1), and find that it resembles the pelagic forms. The specimen reported by Scattergood and Coffin unfortunately disappeared from a public display tank (Scattergood, personal communication). The color they describe suggests a pelagic form. Both of these specimens had probably just settled to the bottom after arrival inshore. Offshore, prejuveniles have been taken by dip-net or other nets at or near the surface. One collection examined indicates that at least the prejuveniles may occur in considerably deeper waters (though they are still pelagic). A series of 24 specimens, 12.4 to 19.9 mm., was collected in an Isaacs-Kidd midwater trawl at 24 fathoms over a depth of approximately 1300 fathoms (see table 1, WHOI collection, Aug. 19–20, 1953). Dr. Richard H. Backus wrote me in August 1958 that this is not a closing net and that "there is no assurance that the catch actually came from 24 fathoms but statistically speaking the chances are great that it did."

South of Cape Hatteras, juveniles and adults are apparently bottom dwellers and show a preference for hard, especially coral or rock, bottoms in depths up to about 60 fathoms (rarely to 110 fathoms). The adults are frequently taken by handlines or traps from in or near rocky areas or hard bottoms. This is particularly true of the larger specimens. It may be that the juveniles just arriving at the bottom from the pelagic habitat may be less restricted in their preferences, as most specimens taken from other than a rock bottom (or one with limited spots for the fish to hide in) were the smaller bottom forms.

The juveniles and adults apparently are very secretive. I have observed this in aquarium specimens, and Winfield Brady of Florida's Gulfarium, Fort Walton Beach, found this to be the case in his observations of wild specimens at depths of about 100 feet. Brady further stated that the fish would remain perfectly motionless in a niche in the rocks while he captured it without the aid of a net.

The preference of *P. altus* for a hard rocky bottom is well illustrated by its distribution in the Gulf of Mexico. The known Gulf distribution of *P. altus* is spotty (fig. 1; tables 1 and 2), as shown through extensive fishing by the U.S. Fish and Wildlife Service throughout most of the Gulf in all depths, in all seasons, and on all types of bottoms. Other collectors' findings substantiate this (table 1). When a chart of this distribution (fig. 1) is compared with the chart of the sedimentary provinces of the Gulf of Mexico as provided by Lynch (1954: p. 79), a similarity is shown (particularly where coral and limestone occur).

The short bigeye probably occurs on the entire Campeche Bank off the north and west coasts of Yucatan and in limited areas in the vicinity of Tampico and Vera Cruz, Mexico (areas of coral and limestone). *P. altus* is known from the entire Gulf coast of Florida, some Alabama and Mississippi waters, and certain areas in the northwestern Gulf (fig. 1)—all areas of hard bottom on Lynch's chart. Off the south Atlantic coast of the United States the bottom in areas where *P. altus* has been most regularly taken is also hard (see Moore and Gorsline, 1960: p. 18). Breaks in the range of *P. altus* in the Gulf correspond to Lynch's charted areas of soft mud bottom. Hildebrand (1954, 1955) did not list this species from shrimp fisheries conducted on soft bottoms in the western Gulf and western Yucatan areas. The West Indian specimens (table 1) were taken in areas where coral and rock are abundant.

Bermuda also furnishes abundant coral or rock substrate.

Temperature is possibly the most basic limiting factor in the distribution of *P. altus*, as the short bigeye is a subtropical or tropical species. Wherever conditions of temperature are suitable, however, the bottom type seems to be especially important in the success of permanent populations of adults.

Specimens are usually taken singly or in twos or threes, but it is not known whether this seeming rarity is a real phenomenon or a false impression gained from the secretive habits of the species as juveniles and adults and from the limited collections of pelagic forms. The collection of a large group of prejuveniles (24 specimens, WHOI collection, Aug., 19–20 1953, table 1) and an even larger series of adults in a single trawl haul (32 specimens, BLBG, *Silver Bay* station 1393, table 1) suggest the latter premise to be correct. Other museum collections from northern waters (table 1) indicate aggregations also, though in these instances data are not specific and complete enough for certainty.

EFFECT OF HABITAT ON METAMORPHOSIS

Results of recent studies (Parr, 1930: p. 58; Hubbs, 1941: p. 184, 1958: p. 282; Breder, 1949: p. 296; and M. C. Caldwell, in press) make it obvious that a wide variety of marine fishes which as adults occupy a bottom habitat have pelagic larvae and prejuveniles which undergo considerable change in appearance in their transition from the pelagic to the bottom habitat. Such stages have frequently been described as separate species or genera (Hubbs, 1958). Furthermore, it has been shown (Breder, 1949) that the specific size (or age) of the individual does not dictate time of change in form, but rather that the environmental change seems to trigger the metamorphosis after the delayed development. The fish maintains its prejuvenile appearance while continuing to grow until, probably within limits, the attainment of suitable conditions of environment. Such an arrested development is known for invertebrate marine animals (Thorson, 1957: p. 482) as well as for fishes (Breder, 1949: p. 296; M. C. Caldwell). As a consequence, a prejuvenile still in its pelagic environment may actually be larger than another of its kind which is in the proper habitat. It is this phenomenon that has resulted in confusion leading to the description of the larger or equally sized prejuvenile of a well-known adult as a separate form.

Pseudopriacanthus altus exhibits such a change of appearance and shows this differential or delayed development related to time of settling to the bottom.

Metamorphic stages in *P. altus* are quite different, and several fisherman told me that there were possibly two species of *Pseudopriacanthus* in the western North Atlantic. One was said to be a "dwarf," which was immediately suspect. The "dwarf" form proved to be merely the prejuvenile stage of *P. altus*. With the differential development in relation to habitat, the "dwarf" form had been seen that was larger than the "normal" form. No large specimens of the "dwarf" form were known simply because they either transformed if the proper habitat was attained or died if it was not. Although a simple method of detecting transitional stages, based on color pattern, was later found, the color pattern would not be particularly noted on casual observation. Hubbs (1958: p. 282) noted that "prejuveniles metamorphose very rapidly into the juveniles, which are much more like the adult. For this reason, transitional specimens are seldom encountered."

Thus, the fishermen had seen either large prejuveniles or transformed specimens of a similar or greater size—the two having quite different appearances. None of the form with the adult appearance was found smaller than about 50–55 mm., which made the validity of the "dwarf" form even more suspect, since this is about the maximum size for the latter. Figure 2 illustrates the two forms in question. They look very different, and as the difference in their standard lengths is only 2 mm., the possibility of two species was reasonable, if one had only these specimens. Note the differences in overall body color, spinous-fin membranes, and especially eye size. These two specimens are extremes of a gradient of general appearance.

It was necessary to find an obvious character, showing the extremes as well as indicating integration, in order to separate the three groups (pretransformed, transforming, and transformed) with relation to size and habitat. The color pattern of the caudal and soft parts of the vertical fins proved useful in this respect. The prejuvenile pattern consists of immaculate or spotted

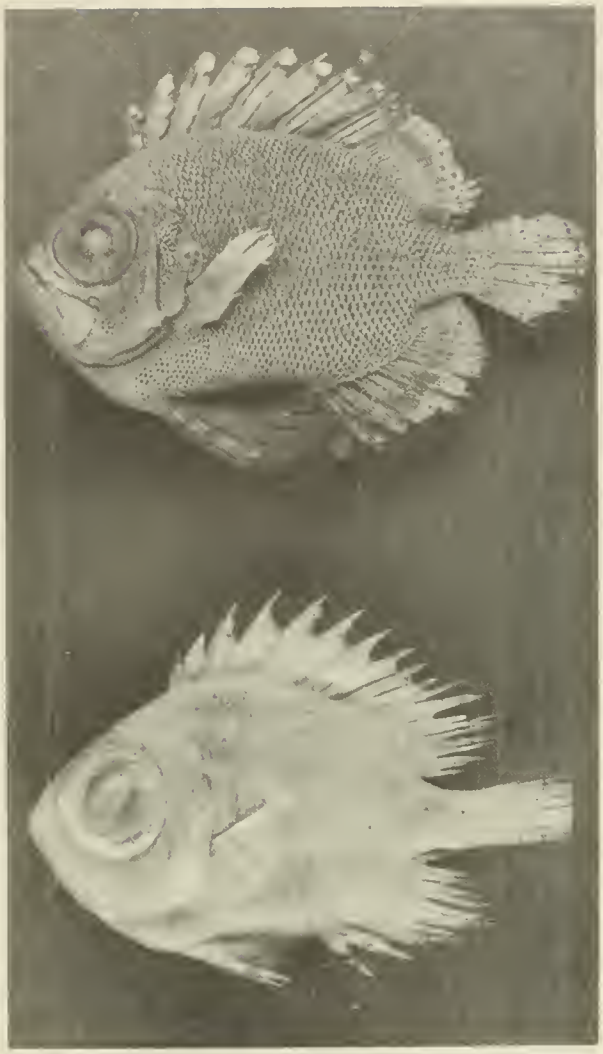

FIGURE 2.—Upper: Large pelagic prejuvenile *Pseudopriacanthus altus* from Massachusetts, showing early metamorphic characteristics (49.3 mm. standard length, CNHM 55986). Lower: Small bottom-dwelling *P. altus* from off St. Augustine, Fla., showing late metamorphic characteristics (47.2 mm. standard length, BLBG).

fins (figs. 16, 17, and 24), while the transformed juvenile and adult pattern shows an immaculate fin with a distinct dark edge (figs. 19–23). Fins on larvae and early prejuveniles are immaculate, and there is no dark edge on fins of a nontransforming late prejuvenile. The transition in color pattern appears to be a migration of the spot-forming pigment to the edge of the fin, where it accumulates to form the dark border. The transition pattern is shown in the two specimens illustrated in figure 2. In figure 3 the specimens which appear as intergrades in fin coloration lie between the specimens showing the extremes in color pattern, and the entire group forms an integrated, though overlapping, series. The individuals from north of Cape Hatteras (table 1) with an integrated fin coloration were taken inshore, and even if washed there, they could have begun the rapid transformation (Hubbs, 1958: p. 282). Most of the individuals from north of Cape Hatteras had the pure pelagic fin coloration (immaculate or spotted, depending on their size), however large they were, further evidence of arrested development (other than increase in size) with maintenance of the pelagic environment. The transforming specimens from the geographical range of the adult usually were trawled or were from inshore situations and thus were probably undergoing successful transformation. Some small spotted-fin bottom specimens, all from the geographical range of the adult, probably had just reached the bottom habitat when collected.

Even within the geographical range of the adult, the size at which the prejuveniles settle to the bottom varies (perhaps based on their geographical origin), for of two specimens collected at the same time (*Silver Bay* station 1299, table 1) the larger (49.4 mm.) retained the pretransformation (spotted) fin coloration, while the smaller (48.6 mm.) exhibited the transitional coloration.

This phenomenon is exhibited in four other collections also, all from Massachusetts. These collections are old, taken without complete and precise ecological and locality data, which precludes definite conclusions as to transitional relationships. The four collections, indicated in table 1, are—

(1) CNHM 55986, 2 specimens, the larger (57.1 mm.) with the pretransformation fin pattern and the smaller (49.3 mm.) with the transforming fin color. (2) USNM 49664, 6 specimens, one of the middle-sized ones (42.4 mm.) with the transforming fin color and the others (30.8, 39.3, 42.9, 44.9, and 47.3 mm.) with the pretransformation pattern. (3) USNM 68129, 4 specimens, the largest and smallest (34.5 and 55.9 mm.) with the transforming fin color and the two middle-sized ones (49.3 and 50.8 mm.) with the pretransformation pattern. (4) USNM 58833, 2 specimens, the larger (41.1 mm.) with the pretransformation fin color and the smaller (35.7 mm.) with the transforming color.

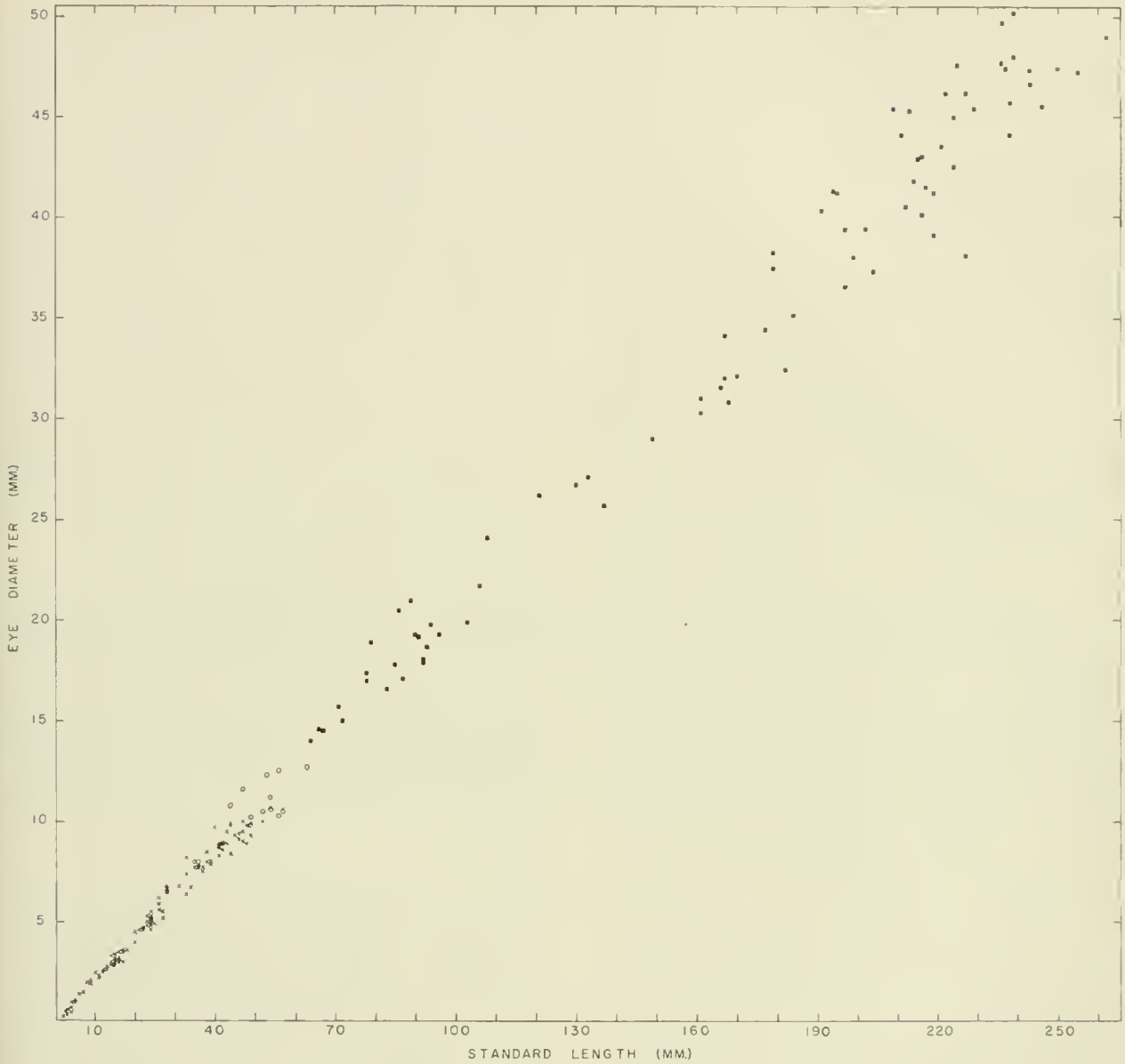

FIGURE 3.—Relation of eye diameter to standard length in *Pseudopriacanthus altus*. (Untransformed larvae and prejuveniles represented by crosses, transforming prejuveniles by open circles, and transformed juveniles and adults by squares.)

No series contained both metamorphosing and metamorphosed specimens.

The largest specimen with the transitional coloration was trawled from 3 fathoms off Soldier Key, Florida (table 1). According to the label, it was estimated to be 2 inches (about 50 mm.) total length at capture (about 40 mm. standard length). The transitional (or transformed) coloration would be expected under those conditions unless the fish had just settled to the bottom when captured. It was then kept in an aquarium at Marineland, Florida, for about 2½ months, and during this time it grew to a total length of 93 mm. (73 mm. standard length). At 73 mm. the fins still retained the transitional coloration, the body remained dark, and the eye was still relatively small. How long the specimen would have retained these transitional features is unknown, but they were retained, under these unnatural conditions, on this much larger speci-

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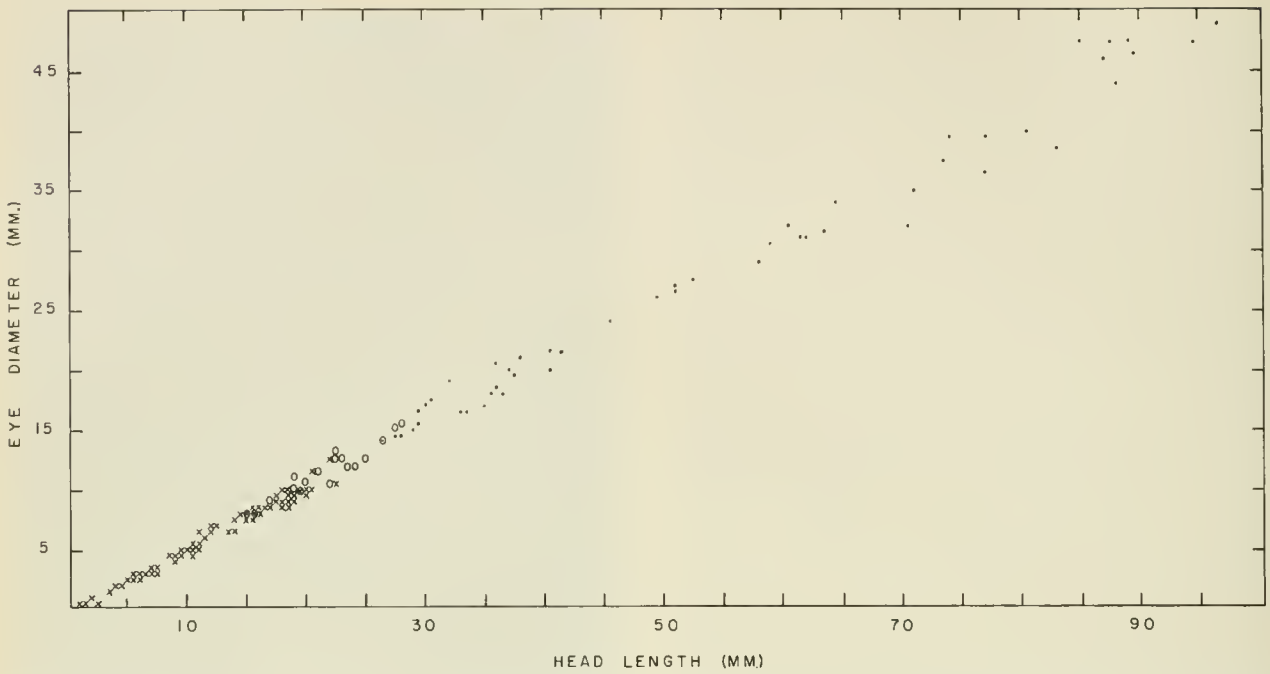

FIGURE 4.—Relation of eye diameter to head length in *Psuedopriacanthus altus*. (Untransformed larvae and prejuveniles represented by crosses, transforming prejuveniles by open circles, and transformed juveniles and adults by small dots.)

men than any found in nature (ca. 65 mm. the largest). The fish was found dead on the floor beside the aquarium, which might suggest that some force drove the transitional individual to seek a more suitable habitat, and that its only method of escape was to leap.

In relation of eye diameter to standard length, there often is a striking difference between the pelagic and bottom forms—the latter having a relatively larger eye at comparable sizes. Also, regression lines estimated visually show that the increase in eye diameter per unit of increase both in length of fish (fig. 3) and in length of head (fig. 4) is greater in the smaller (pelagic) fishes than it is in the larger (bottom) forms. Rather than there being an inflection in the zone of transformation (about 35 to 65 mm.), there appears to be a step, the result of a very rapid and apparently sudden increase in relative (as well as actual) eye size during transformation. The fish assume the bottom habitat at different sizes, and it is in the size range of the transformation that *P. altus* changes from a pelagic to a bottom habitat. Once the relative size of the eye reaches its maximum—in the size range (35–65 mm. standard length) at which the bottom habitat is assumed—it maintains a constant rate of increase (but lower than initially) to the largest size, though the eye diameter may be relatively smaller in larger fish than in the pelagic young.[1]

Figure 5 demonstrates the relation of eye size to habitat, length of the fish, and stage of development suggested by fin coloration. The open circles represent specimens dip-netted, surface-netted, or washed ashore. The solid squares represent specimens either demonstrated or suggested to have come from a bottom habitat. A few nontransformed specimens taken from a bottom habitat are indicated by open squares. Transitional stages from each habitat, as determined on fin color pattern, are represented by half-solid symbols. The dashed line suggests the dividing line between pelagic and bottom-dwelling specimens, with a few exceptions among bottom forms.

It is evident that pelagic individuals not finding suitable habitat continued to grow and may exceed in length the bottom-dwelling in-

[1] Some of the smallest larvae (fig. 5) have a much smaller eye in relation to standard length than most of the adults, but as they differ so from the adults in many features they are omitted from this discussion.

dividuals, as discussed earlier. Despite a wide range of eye diameters, particularly in the larvae (about 5 mm. or less), in which they may be influenced by physical distortion of the specimens, the eyes of pelagic specimens generally are relatively smaller than those of bottom-living ones. Transforming bottom forms plot generally lower on the graph than pelagic forms of the same size. Whether this increase in relative eye size with change of habitat is cause or effect is not known, though I favor effect (or the need for a larger eye in the dimly lit zone which the adult usually inhabits as compared with the brightly lit surface waters occupied by the larvae and prejuveniles). It is not clear what processes trigger the descent of the fish to the bottom.

These offshore-caught forms were taken at or near the surface (both the larvae and prejuveniles), except for a group taken by a midwater trawl set at 24 fathoms over 1,300 fathoms (table 1). These individuals, well north of the range of the adult (fig. 1), might have been seeking the bottom. Perhaps the stimulus in this case is light—with the fish changing from a positive to a negative phototropic response. This might also initiate the increase in relative eye size, to compensate for the reduced illumination. A change in dietary requirements and the pursuit of food also may influence the change of habitat in that the new requirements are met only in the bottom habitat.

The differential rate of growth (previously noted) related to habitat is well illustrated by the material examined. The largest actual or inferred pelagic forms (up to 58 mm.) were taken in northern Atlantic waters (table 1), which suggests they continued to grow without changing form as they were carried north by the Gulf Stream. The large pelagic form illustrated in figure 2, from Massachusetts, is one of these; while the small, nearly transformed bottom form is from about 10 fathoms, off St. Augustine, Florida, or well within the range of the adult.

The smaller pelagic forms taken in northern Atlantic waters could easily have been spawned in the northern part of the range of the adult and not yet had time to reach a large size. Prejuveniles taken in southern latitudes in the Atlantic (table 1) are all small (maximum size about 20 mm.), suggesting that they had been spawned from nearby adults or had found their way to an inshore bottom to transform rather

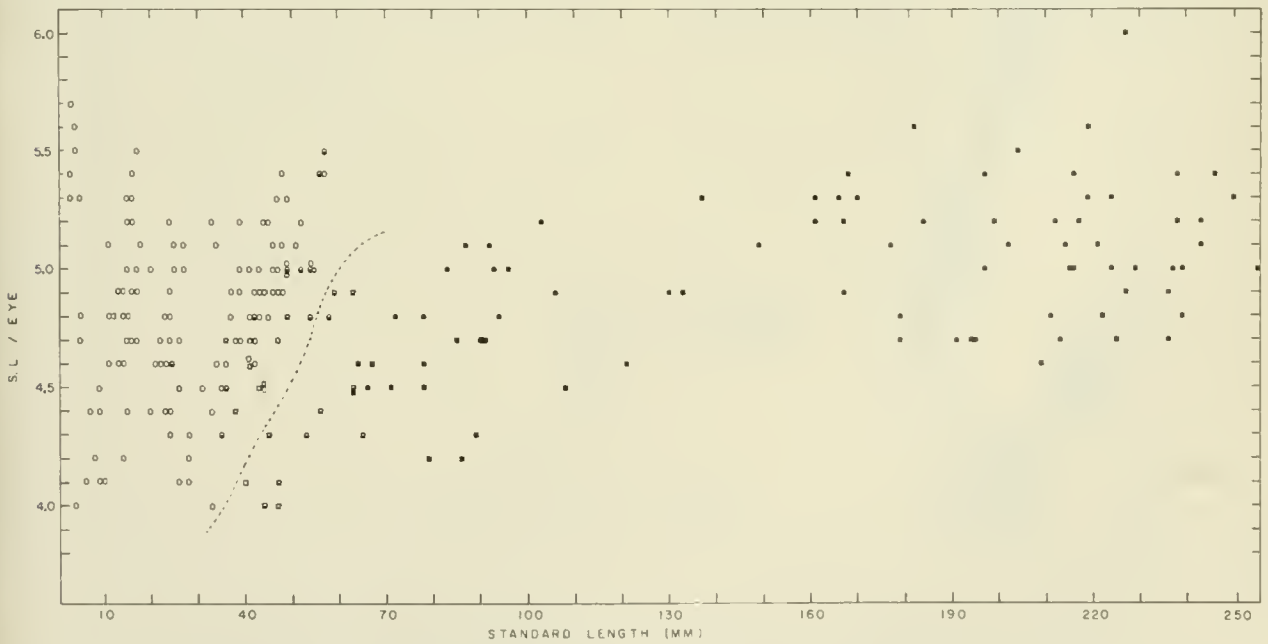

FIGURE 5.—Relation of ratio of eye diameter in standard length to standard length in *Pseudopriacanthus altus*. (Untransformed pelagic larvae and prejuveniles represented by open circles, untransformed bottom-living prejuveniles by open squares, pelagic transforming prejuveniles by half closed squares, and transformed juveniles and adults by closed squares.)

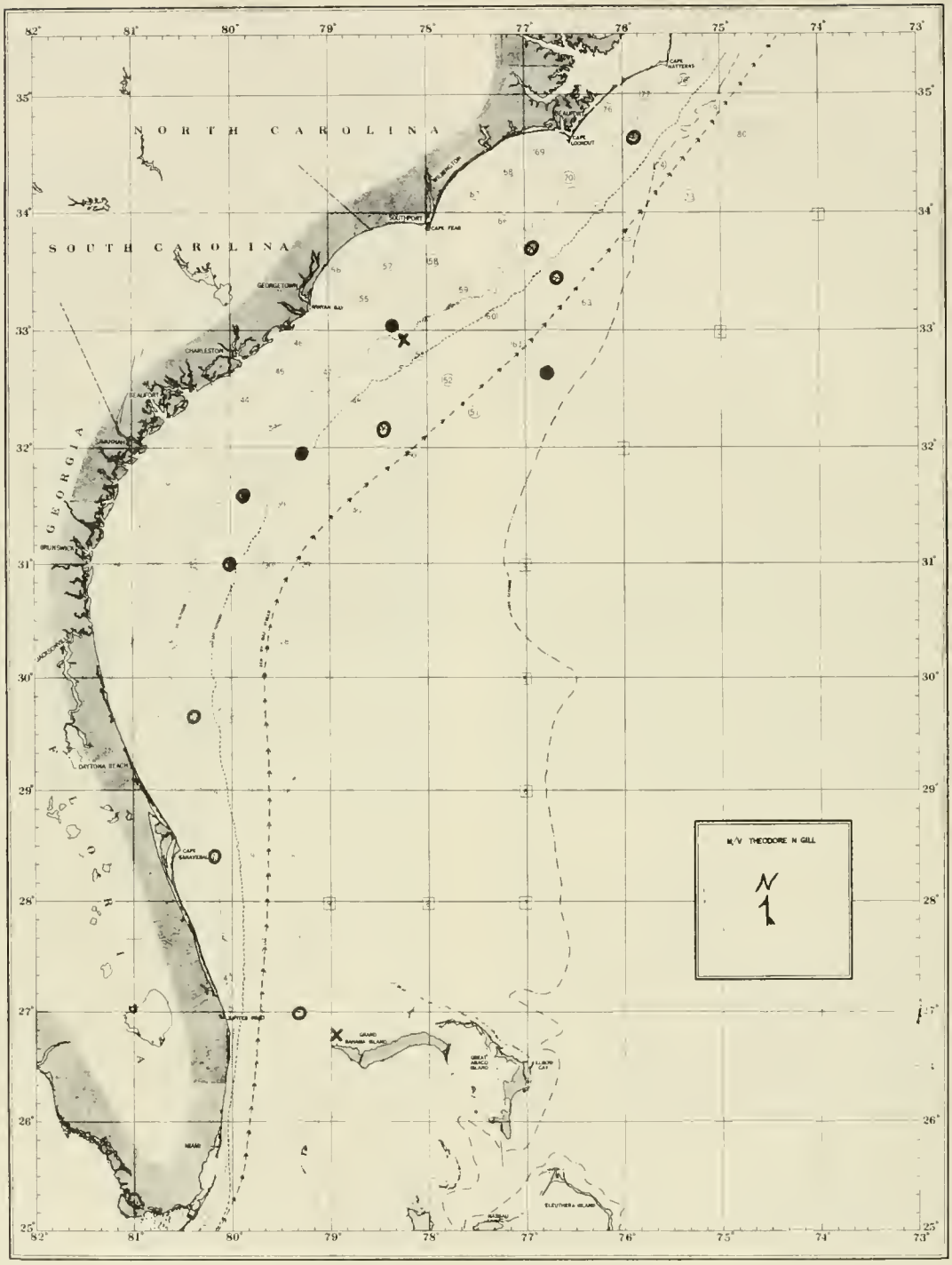

FIGURE 6.—Locations of capture of larval and small prejuvenile *Pseudopriacanthus altus* from operations of the M/V *Theodore N. Gill* off the southeastern Atlantic coast of the United States. Indicated to the seaward off the central coastline are the 20-fathom contour, the 100-fathom contour, the approximate axis of the Gulf Stream, and the 1,000-fathom contour. Open circles represent captures of one or more larvae, closed circles, one or more 15-mm.-or-less prejuveniles, and crosses prejuveniles from stomach contents. See table 1 for exact locations, numbers, and sizes of *Gill*-caught material.

than be swept north of the range of the adult. Once north of Cape Hatteras, they would find themselves generally in too deep water to transform until they reached the coasts of New Jersey, Long Island, or Cape Cod. There, prolonged life is probably impossible due to temperature. Likewise, pelagic forms taken in the Gulf of Mexico are small; however, there is much suitable habitat within this semienclosed area to provide proper temperature, depth, and substrate for the prejuveniles to settle in and transform successfully.

SPAWNING

TIME OF SPAWNING

Larvae collected during the *Gill* operations give some indication of the time of spawning of *P. altus*. The smallest specimen (2.2 mm.) was taken on July 25 off the east coast of southern Florida at regular station 1 on *Gill* cruise 3 (table 1; figs. 6 and 7). Individuals of comparable size were taken at other stations and on subsequent cruises through the middle of September (table 1; fig. 7). Such small specimens must have been only a few days old at most, and probably only a day or so. While they indicate that the spawning season for this species must extend for at least 2 months, from mid-July to mid-September, 8.6- and 8.7mm. specimens taken July 6 off North Carolina at regular station 62 on *Gill* cruise 7 indicate an even more extended season. To reach this size probably took at least several days, which extends the spawning season back to early July or perhaps late June. Gordon (1960: p. 61) noted the collection of a 62-mm. total length individual in Rhode Island in July, indicating a still somewhat earlier initial spawning, at least in some years, for this specimen to have reached this size by even late July (fig. 7). Specimens taken after mid-September were 10 mm. or more (table 1; fig. 7), indicating completion of the spawning season. Further evidence for a midsummer to late summer or early fall spawning in southern latitudes is seen in table 1.

Several 20- to 30-mm. specimens were taken in northern latitudes in the late summer and early fall. These were not included in figure 7 because only partial data, such as a month or spread of 2 months, were given on labels. There are also numerous references in the literature to late summer and fall collections of small (prejuvenile) specimens in New England and slightly more southern waters and to their apparent arrival there via the Gulf Stream.

Still further evidence that spawning is completed by mid-September at the latest is given by a

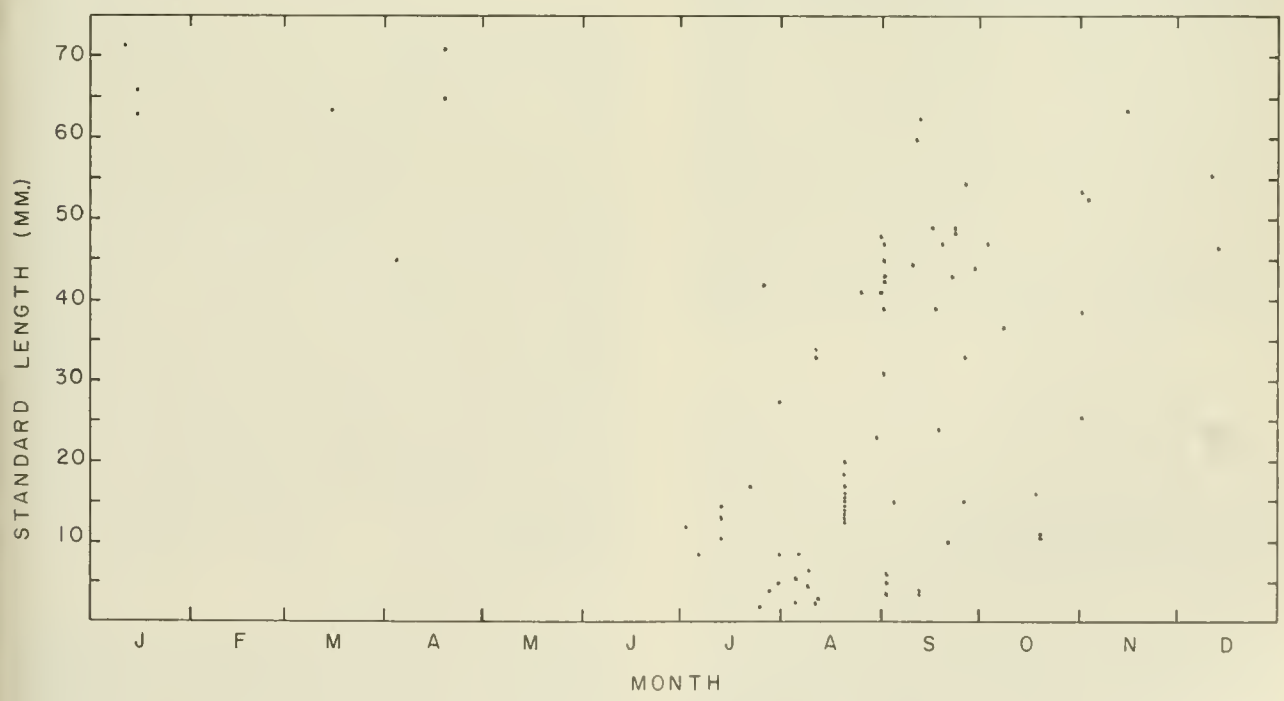

FIGURE 7.—Size distribution, by months, of specimens of *Pseudopriacanthus altus*, 75 mm. standard length or less.

series of 32 presumably spent adult specimens (161.0–261.8 mm.) taken at *Silver Bay* station 1393 on October 26 (table 1).

PLACE OF SPAWNING

From all evidence, *P. altus* is a very secretive and sedentary species unlikely to undertake major spawning migrations, if it moves at all. The adults seemingly spawn where they spend their mature life, in waters of about 60 fathoms or less (table 1), rarely to 110 fathoms. Collections from the *Gill* show that the larvae are pelagic. Although sampling was conducted from near the shore out into the approximate axis of the Stream (Anderson, Gehringer, and Cohen, 1956), most of the larvae were taken westward of the Gulf Stream (fig. 6) over depths of less than 100 fathoms, mostly 20–30 fathoms (table 1). Likewise specimens dip-netted in southern latitudes (below Cape Hatteras) were taken to the shoreward, except for those taken nearer the middle of the Gulf Stream in higher latitudes south of Cape Hatteras and one taken on the eastern side of the Stream northwest of Grand Bahama Island (table 1; fig. 6). The latter individual could have been spawned along the western edge of the Bahama Islands, or even in the northern Antilles, and reached its point of capture, despite its small size (2.2 mm.), in the fast flow of the Gulf Stream in this region (Leipper, 1954). The larvae taken in the main Stream off the Carolinas (table 1; fig. 6) from farther offshore could have had a similar origin, or could have originated in inshore continental waters and been transported much farther offshore after spending several days in the vagaries of the flow. Prejuveniles taken well offshore north of Cape Hatteras presumably could have had either a southern inshore continental origin or one in the West Indies or Bahamas.

MORPHOLOGY

Detailed descriptions of morphological features not discussed in this paper may be found in Jordan and Evermann (1896: p. 1239), Smith (1907: p. 285), Hildebrand and Schroeder (1928: p. 254), and Morrison (1890: p. 163).

Larvae of other Priacanthidae were taken in *Gill* tows, and series of these (*Priacanthus*) were distinguished from *Pseudopriacanthus altus*. Larval *P. altus* (see figs. 8-10 and descriptions of larvae in following section) could be distinguished from larval *Priacanthus* of comparable size by the presence of heavy pigment on the dorsal aspect of the brain and on the dorsal surface of the gut, a series of many small dark spots on the ventral midline as opposed to series of only a few spots (less than 10 at the smallest sizes) on *Priacanthus*, pigmented gill arches at certain sizes, and by shorter preopercular spines (half the length of those in *Priacanthus*).

As with most marine fishes having truly pelagic larvae distributed by ocean currents (a phenomenon which permits free exchange of genes), *Pseudopriacanthus altus* exhibits no measurable or significant geographical variation, but apparently is constant throughout its range. As a partial exception, the 108.3-mm. specimen from the Virgin Islands (table 1; appendix table A–1), representing a population so placed geographically that it receives little or no gene influence from other areas, exhibited characters which fell within the range of meristic values for the species, but approached the extremes of several specimens (low gill-raker count of 6+17; high lateral-line scale count of 37; high vertical scale-row count of 41; and a high pectoral-ray count of 19 left and 18 right). In body proportions it appeared normal.

MERISTIC CHARACTERS

Counts were recorded only on prejuveniles, juveniles, and adults. As, by my definition, the full complements of all fin rays are not formed in larvae, the numbers of spines and soft-rays were not recorded for larvae. The progression of development, however, is discussed under each character—scale, fin-ray, and gill-raker formation was very rapid, once initiated. The smallest specimen for which counts were recorded and included in the tables was 8.2 mm. It was considered the earliest prejuvenile. The next smaller specimen available, 6.6 mm., although complete in complement of other fin-rays, did not have a full complement of secondary caudal rays. This specimen was considered the largest larva of the study. The point of division between larvae and prejuveniles, by my definition, lies between 6.6 and 8.2mm.

Fin and Fin-Ray Development

Parts of the rays of many fins of critical-sized specimens were missing. Therefore, the terms "at least" and "about" are used in the following

discussions, as the precise size at which a character developed could not be determined. Complete segmentation and complete branching indicate at least one segmentation line or one branch in each ray (which segments or branches) of the fin.

Caudal fin.—Development of the hypural complex began at about 3.5 mm. The turned-up urostyle was still obvious at 6.6 mm. and development of the hypural was complete before 8.2 mm. Ossification was first noted in a 4.0-mm. individual.

In the development of the caudal fin, a finfold was present in the smallest larva (2.2 mm.; see fig. 8), and rays apparently were forming, although no ossification of rays was noted in stained specimens until a size of 3.5 mm. Ossification proceeded anteriorly, and the full complement of 16 principal rays was evident in a stained 4.4-mm. larva. Segmentation, beginning with the innermost rays, had begun by at least 4.4 mm., and was completed by at least 8.2 mm. Branching had begun at 10.2 mm., and was complete at 16.8 mm. Four dorsal and four ventral ossified secondary rays were present for the first time at 8.2 mm. Large adults showed, by gross microscopic examination, all secondary rays to be segmented.

All 121 caudal fins so examined had 14 branched principal soft-rays and two unbranched principal soft-rays (the most-dorsal and-ventral principal rays of the fin). The principal rays are divided equally between the two caudal lobes.

Pectoral fins.—A pectoral-fin membrane (fold) with forming rays was present in the smallest larva (2.2 mm.; see fig. 8). Ossification, shown by staining, began ventrally at about 3.5 mm. There were 13 rays in the pectoral fin of a 4.4-mm. larva, 15 in one of a 4.8-mm. larva, and 17 were seen in a 5.3-mm. individual. Segmentation had begun by at least 6.6 mm., starting with the uppermost rays, and was complete by about 8.2 mm. Neither the size at which branching began, nor the sequence, could be determined, but it was complete by 8.2 mm. In large individuals the most-dorsal and two most-ventral rays are unbranched.

The variation in number of pectoral rays of the full complement is shown in table 3. In addition, three other individuals had 17 left pectoral rays (the right rays were not counted). Large series

TABLE 3.—*Variation in pectoral fin-ray counts for 138 pairs of fins in* Pseudopriacanthus altus

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

LEFT \ RIGHT	16	17	18	19	Total
16	1 (0.7)				1 (0.7)
17	1 (0.7)	81 (58.7)	7 (5.1)		89 (64.5)
18		3 (2.2)	43 (31.2)		46 (33.3)
19			1 (0.7)	1 (0.7)	2 (1.4)
Total	2 (1.4)	84 (60.9)	51 (37.0)	1 (0.7)	138

of specimens contained individuals with both the 17–17 and 18–18 counts, as well as ones with unlike combinations. Some juvenile and adult fish had 17 or 19 rays, but the usual count was 18, while the predominant count for prejuveniles was 17, with two specimens having 16.

Dorsal fin.—A finfold was present posteriorly at 2.6 mm., and there was a complete fold in a 2.7-mm. specimen. No ossified rays were found in stained specimens until 3.5 mm.; and ossification proceeded posteriorly. A full complement of ossified rays, distinguishable as pro-spines and pro-soft-rays, was present in a 4.4-mm. stained specimen. Segmentation of pro-soft-rays began at about 6.6 mm., starting with the posteriormost rays, and was complete by at least 8.2 mm. No soft-rays were branched at 15.0 mm., but some posterior ones were branched at 16.8 mm., and branching was apparently complete at 20 mm., and certainly at 34.0 mm.

The full complement of dorsal spines, 10 (X), found in all 233 prejuvenile, juvenile, and adult specimens so examined, was present by 8.2 mm. (the earliest prejuvenile of the study), when segmentation of the soft-rays was complete. Variation in the number of fully developed soft-rays is summarized in table 4.

TABLE 4.—*Variation in dorsal and anal fin-ray counts for 233 specimens of* Pseudopriacanthus altus

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

NUMBER \ COMBINATIONS OF FIN-RAY COUNTS (DORSAL; ANAL)	X, 10; III, 10	X, 11; III, 9	X, 11; III, 10	X, 11; III, 11	X, 12; III, 11
	12 (5.2)	3 (1.3)	216 (92.7)	1 (0.4)	1 (0.4)

Anal fin.—A finfold was present at 2.6 mm., and a full complement of rays was seen at 4.4 mm. (pro-spines and pro-soft-rays distinguishable). The first ossified rays were seen in stained specimens at 3.5 mm.; and ossification proceeded posteriorly. Segmentation of pro-soft-rays was first seen at 5.3 mm., and was complete by about 8.2 mm. There was no branching of anal rays in a 13.9-mm. individual, but branching had begun with the most posterior rays at 15.0 mm., and was complete by 16.8 mm.

The full complement of anal spines, three (III), found in all 233 prejuvenile, juvenile, and adult specimens so examined, was present by 8.2 mm., when segmentation of the soft-rays was complete. Variation in the numbers of fully developed soft-rays is shown in table 4. The anal fins of individuals with a dorsal count other than the modal X, 11 show the modal anal ray count of III, 10 in all but one instance (a specimen with a dorsal-ray count of X, 12 and an anal-ray count of III, 11).

Pelvic fins.—This was the last fin to form, there being no evidence of it until a bud appeared in a 3.9-mm. specimen. Ossified rays were first formed in a 4.0-mm. specimen, but the full complement of 6 (distinguishable as 1 pro-spine and 5 pro-soft-rays) was not present until 4.8 mm. Segmentation was first noted by about 6.6 mm., and was complete by about 8.2 mm. Branching had started by 8.2 mm., and was complete at 8.7 mm.

All pelvic fins so examined, 147 pairs, had a count of 1 spine and 5 soft-rays, except for the right fin of a 45.5-mm. specimen (from USNM 58831), which had a 1, 4 count. Such a variant is extremely unusual in this constant-rayed fin, and the low count was possibly due to an injury to the embryo.

Scales

Although the smallest prejuvenile (8.2 mm.) was completely covered with scales, the smallest individual on which vertical scale rows were counted was 23.8 mm., and the smallest on which lateral-line scales were counted was 26.4 mm. The full range of adult complement of vertical scale rows and pored lateral-line scales was present at approximately these sizes. On the basis of a previous discussion of the phenomenon

TABLE 5.—*Variation in counts of pored lateral-line scales and vertical scale rows in 145 specimens of* Pseudopriacanthus altus

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

VERTICAL SCALE ROWS	PORED LATERAL-LINE SCALES									
	31	32	33	34	35	36	37	38	39	Total
35	1 (0.7)	1 (0.7)	1 (0.7)	2 (1.4)						5 (3.4)
36		2 (1.4)	1 (0.7)	3 (2.1)						6 (4.1)
37	1 (0.7)	3 (2.1)	4 (2.8)	9 (6.2)	4 (2.8)	2 (1.4)	1 (0.7)			24 (16.6)
38	1 (0.7)	2 (1.4)	10 (6.9)	5 (3.4)	14 (9.7)	4 (2.8)	3 (2.1)			39 (26.9)
39			9 (6.2)	8 (5.5)	8 (5.5)	6 (4.1)	2 (1.4)	1 (0.7)		34 (23.4)
40			2 (1.4)	11 (7.6)	5 (3.4)	1 (0.7)	4 (2.8)		1 (0.7)	24 (16.6)
41			1 (0.7)	1 (0.7)	3 (2.1)	1 (0.7)	1 (0.7)	2 (1.4)		9 (6.2)
42		1 (0.7)		1 (0.7)	1 (0.7)					3 (2.1)
43					1 (0.7)					1 (0.7)
Total	3 (2.1)	9 (6.2)	28 (19.3)	40 (27.6)	36 (24.8)	14 (9.7)	11 (7.6)	3 (2.1)	1 (0.7)	145

(Caldwell, 1957: p. 105), I presume that once the scales are formed in *P. altus*, the number for that individual remains unchanged. The variation in combinations of numbers of vertical rows and pored lateral-line scales is shown in table 5.

No scales had formed at 4.8 mm. At 5.3 mm., there were small patches on the lower flank of the belly on each side in the region anterodorsal to the anus, and a small patch near the anterior end of the isthmus. A 6.6-mm. individual was covered with scales except for areas just ventral and posterior to the base of the pectoral fins, on the lower half of the caudal peduncle, and the lower half of the flank of the body above the anal fin and behind the anus. The scales appeared to form first as widely spaced bristles. These soon developed into the upstanding ctenii of the prejuvenile, and in final development they were strongly ctenoid scales firmly anchored in the scale pockets.

The lateral-line scales did not form until about 25 mm. There was an open channel between the other scales (seen in an 8.2-mm. individual) to mark its course in the smaller fish. The scales adjacent to this channel appeared to join to cover the open area as they enlarged, meanwhile developing the pores.

Gill Rakers

The smallest specimen in which gill rakers were counted was 19.9 mm. The count obtained, 8 + 19, falls at the mode of the range for the adults. Variation in combinations of upper-limb and lower-limb gill rakers is summarized in table 6.

Although the size at which gill rakers first form was not determined, they were well-developed in the smallest prejuvenile of 8.2 mm.

TABLE 6.—*Variation in upper- and lower-limb gill-raker counts for 112 specimens of* Pseudopriacanthus altus

[The upper number in each block is the count obtained for that combination, and the number in parentheses below is the approximate percentage of that count in the total sample]

LOWER LIMB	UPPER LIMB 6	7	8	9	Total
17	1 (0.9)	3 (2.7)	2 (1.8)		6 (5.4)
18		11 (9.8)	10 (8.9)		21 (18.8)
19		7 (6.3)	27 (24.1)	2 (1.8)	36 (32.1)
20	1 (0.9)	3 (2.7)	32 (28.6)	9 (8.0)	45 (40.2)
21		1 (0.9)	1 (0.9)	2 (1.8)	4 (3.6)
Total	2 (1.8)	25 (22.3)	72 (64.3)	13 (11.6)	112

Bony Cranial Crest

A single prominent, medial, cranial crest, armed throughout its length with 8 strong dorsomedial serrations, and with a sharply upturned (about 40°) backward projection, was present on a 2.2-mm. individual (fig. 8). At 2.4 mm., the serrations had increased in number and become less prominent, while the backward projection had begun to decrease its angle and lie flatter against the head and body. By 2.6 mm., the serrations were lost on the anterior part of the crest and were weak on the backward projection

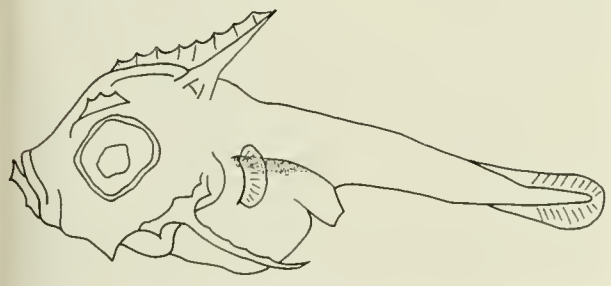

FIGURE 8.—Larval *Pseudopriacanthus altus*, 2.2 mm. standard length (BLBG, *Gill* Cr. 3, Reg. 1), Semidiagrammatic.

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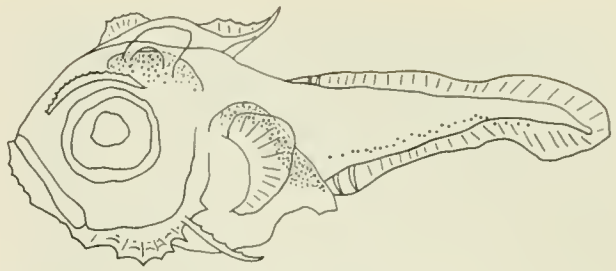

FIGURE 9.—Larval *Pseudopriacanthus altus*, 3.2 mm. standard length (BLBG, *Gill* Cr. 3, Reg. 75). Semidiagrammatic.

(which by this size was flat against the dorsal surface of the body except for its still-upturned tip). At 3.2 mm. (fig. 9), a small, weakly serrate, secondary crest had appeared on the anterior median surface of the original crest. A compressed secondary crest also had formed at the angle made by the upturned projection. By 6.6 mm. (fig. 10) this crest had expanded to include the entire length of the original crest. Strong serrations, each supported by a thickening to the foundation formed by the original crest, extended along the top of this secondary crest (fig. 10). By 8.2 mm.,

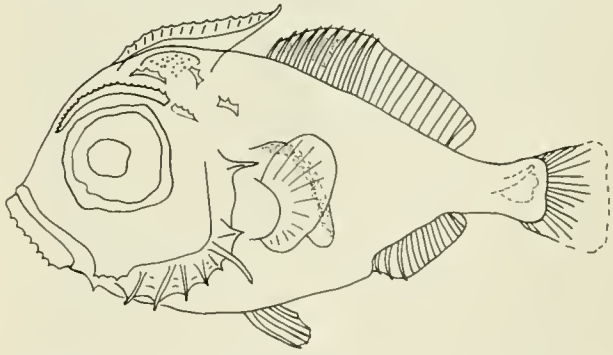

FIGURE 10.—Larval *Pseudopriacanthus altus*, 6.6 mm. standard length (BLBG, *Gill* Cr. 3, Reg. 49). Semidiagrammatic.

the serrations had become weaker, and the entire crest had begun to be absorbed by overgrowth of the dorsal surface of the head. Only a row of weak serrations in the midline of the forehead remained in a 16.8-mm. specimen, an outline only by 19.9 mm., and all trace had disappeared in a 34.0-mm. individual.

Supraocular Crest

Larval and early prejuvenile *P. altus* possess an eyebrowlike serrate bony crest over each eye.

In the smallest larva, 2.2 mm. (fig. 8), this crest bore three heavy serrations and extended over only the anterior half of the supraocular region. At 2.7 mm., this crest extended both posteriorly and anteriorly over the entire top of the eye and beyond. The serrations had increased in number but decreased in strength. By 3.9 mm., the crest extended farther around the eye to shield its anterodorsal and posterodorsal arcs. By 6.6 mm. (fig. 10), the serrations and the ridge itself were becoming decreasingly prominent, and additional serrate ridges were forming lateral to the medial cranial crest. By 8.2 mm., the supraocular crest had become more finely serrate and the additional ridges were more prominent. By 12.1 mm., (fig. 11) all of these crests and ridges were disappearing (probably being overgrown as they ceased to grow), and by about 35 mm. only vague outlines could be seen. These, too, were lost by 40 mm.

Preopercular Spines

Larval *P. altus* possess a strong, conspicuous, ridged, and serrate spine at the angle of the preopercle, flanked by two spines that are shorter and less prominent (but also ridged). In the 2.2-mm. larva (fig. 8), the angle spine reached nearly to the anal opening. It became progressively shorter in relation to the head length as the size of the fish increased (actually it appeared to be overgrown as the preopercle enlarged), until in individuals of about 75 mm., it remained only as a heavy, pointed projection, little more conspicuous by its length than its immediate neighbors above and below. Although its outlines were still discernible in the largest adult examined (261.8 mm.), it lost its significance as a spine in fish above about 75 mm. Beginning with the largest larvae, and as the fish enlarged, other spines also developed as strong serrations on both limbs of the preopercle, including the two shorter spines which originally flanked the angle spine. The serrations increased in numbers and strength with length of fish to about 200 mm., after which they decreased. The preopercle of the largest adults is only finely serrate and the larger angle spines are overgrown and visible only as outlines.

Nostrils

Formation of the paired nostrils was complete (including a tube surrounding the opening of the more anterior one of a pair on each side) in an 8.2-mm. specimen. No external openings were discernible in a 6.6-mm. individual.

Teeth

Adults of *P. altus* possess irregular rows of small canine or sharp-pointed peglike teeth on the premaxillaries and dentaries. Similar small peglike teeth also occur on the tongue, vomer, and palatines. The size at which these teeth form was not determined, but all teeth were present and obvious in a 19.9-mm specimen.

At about 35 mm., a single row of rather widely spaced canines, several times the size of their neighbors, began to develop on the outer edge of the premaxillaries and dentaries. As they first appeared at about the size metamorphosis begins, before the bottom habitat is assumed, and persisted through the largest specimens examined, their appearance may be related to a new diet.

Fin-Ray Serrations

The spines of the dorsal, anal, and pelvic fins of the smallest prejuveniles develop ridges which become rough due to small irregular projections. These projections develop on the leading edge of the single pelvic spine, and on alternate lateral aspects of the dorsal and anal spines. The dorsal and anal spines are heteracanthus (staggered) in their insertions, and a spine that is heavy and rough on its left side is more delicate and smooth on its right. The next spine following is rough on its right side and smooth on its left. In the larger adults, the roughness tends to disappear, though the alternating rough and smooth appearance persists.

The dorsal, anal, and pelvic soft-rays in the smallest prejuveniles also develop the rough surface on both sides, and this character persists in lessening degree in the larger specimens examined, though it is never completely lost.

Branchiostegals

A full complement of six branchiostegal rays on each side was evident on a 2.7-mm. specimen, the smallest stained.

Vertebrae

Ossification was first noted in the anteriormost vertebrae in the smallest specimen (2.7 mm.) stained. All vertebrae in a 4.8-mm. individual showed some degree of ossification, which progressed posteriorly.

BODY PROPORTIONS

Twenty-five body parts were measured on a complete size range of specimens from the largest larva (6.6 mm.) to the largest adult (261.8 mm.) and the data presented in table A–1. Selected measurements were made on 158 additional specimens from the smallest larva (2.2 mm.) to a 254.9-mm. individual (table A–1). These measurements were plotted relative to standard length, and the resulting scatter diagrams are included in figures 3 and 25 to 32. Regression lines were eye-fitted to the data with a straight-edge for discussion purposes, but were not included in the figures. All proportions of larvae were not measured because most of the characters included here are based on parts not present in larvae or because the larvae are so unlike the prejuveniles that to include them would be of little value. The larvae are illustrated in figures 8 to 10.

The distances from pelvic-fin insertion to snout and to midcaudal base were not measured, as the insertion of this fin remained constant in position with that of the pectoral.

Eye diameter in relation to head length and to standard length was discussed in detail in an earlier section on metamorphosis in relation to change of habitat. The eye diameter initially has a higher rate of increase than in sizes greater than about 35–65 mm., the zone of transformation (fig. 3). The relation of eye to head remains constant at all sizes, after an upward step at metamorphosis (fig. 4).

FIGURE 11.—Pelagic prejuvenile *Pseudopriacanthus altus*, 12.1 mm. standard length (BLBG, *Gill* Cr. 7, Reg. 38).

FIGURE 12.—Pelagic prejuvenile *Pseudopriacanthus altus*, 15.0 mm. standard length (BLBG, *Gill* Cr. 8, Reg. 54).

Many of the regression lines eye-fitted to the body proportions in standard length show inflections at various sizes (step indicated in parentheses); some show no inflection. The body proportions are as follows:

Body depth at pelvic-spine base, down (75–85 mm.), figure 25; body depth at third anal-spine base, down (75–85 mm.), figure 25; head, down (125–135 mm.), figure 32; snout to dorsal-fin origin, down (120–130 mm.), figure 30; snout to dorsal-fin termination, down (75–85 mm.), figure 30; snout to anal-fin origin, no inflection, figure 30; postorbital, down (80–90 mm.), figure 32; least depth of caudal peduncle, down (150–160 mm.), figure 29; dorsal-fin origin to midcaudal base, down (95–105 mm.), figure 29; anal-fin origin to midcaudal base, down (95–105 mm.), figure 29; dorsal-fin base, down (65–75 mm.), figure 32; anal-fin base, down (80–90 mm.), figure 32; bony interorbital, down (50–60 mm.), figure 31; pectoral fin origin to snout, down (110–120 mm.), figure 31; pectoral fin length, down (95–105 mm.), figure 31; pelvic-fin spine length, down (150–160 mm.), figure 28; second pelvic-fin soft-ray length, down (100–120 mm.), figure 28; maxillary, down (120–130 mm.), figure 30; third dorsal-fin soft-ray, down (step at 70–80 mm.), figure 27; third anal-fin soft-ray, down (70–80 mm.), figure 27; snout, up (50–60 mm.), figure 30; dorsal-fin termination to midcaudal base, up (110–130 mm.), figure 26; anal-fin termination to midcaudal base, up (110–130 mm.), figure 26; and pectoral fin

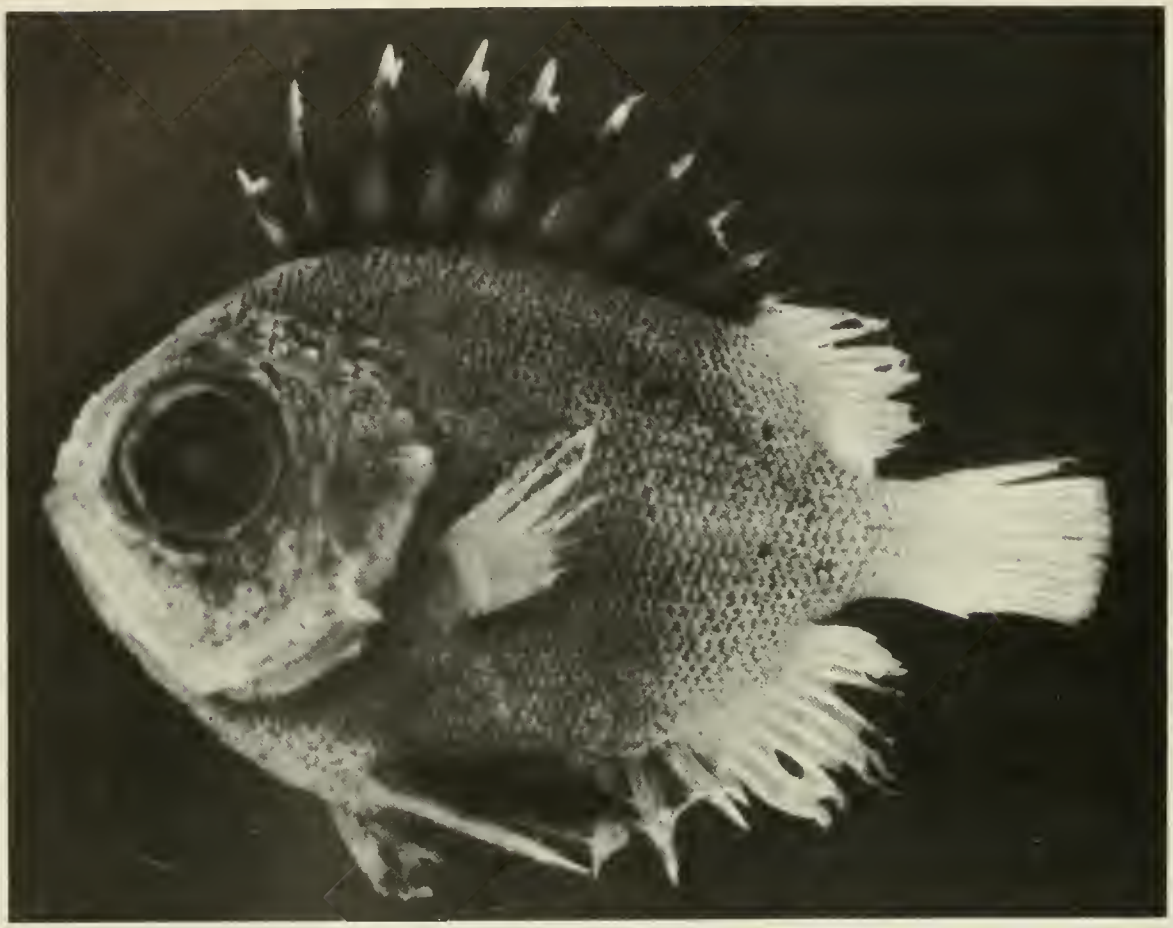

FIGURE 13.—Pelagic prejuvenile *Pseudopriacanthus altus*, 16.8 mm. standard length (WHOI).

origin to midcaudal base, up (130–140 mm.), figure 29.

Although the data are not sufficiently strong to support a positive statement, I believe from examination of a size series of specimens (figs. 11 to 23) that the inflections in relations of body proportions to standard length are, at least in part, a function of a general posteranial elongation of the larger fish, particularly in the region of the caudal peduncle, brought about by a disproportionately greater rate of increase in length in comparison with increase in body part—rather than a slowing down of growth in the body part and a constant rate of increase in the length.

PIGMENTATION

PIGMENTATION OF PRESERVED SPECIMENS

The following descriptions are based on pigmentation of formalin- and alcohol-preserved specimens. In the discussion which follows, the word "pigmentation" refers only to dark chromatophores, which appear brown or black. These chromatophores remain, though varying in intensity with type and duration of preservation, for an indefinite, usually a long period of time and to systematists are the most useful of all pigment characters.

The eye remains dark throughout life.

Body Pigmentation

Pigmentation in the smallest specimen examined, 2.2 mm. (fig. 8), consisted only of (1) a few internal scattered chromatophores either on the upper exterior surfaces of the gut, or on the lining of the abdominal cavity, and (2) dark areas extending either across the anterior and posterior portions of the optic lobes or on the brain case, forming a pigmented area under the single cranial spine. In addition, a small patch of pigment extended between the eyes, across the surface of the forebrain, anterior to the optic-lobe pigmentation.

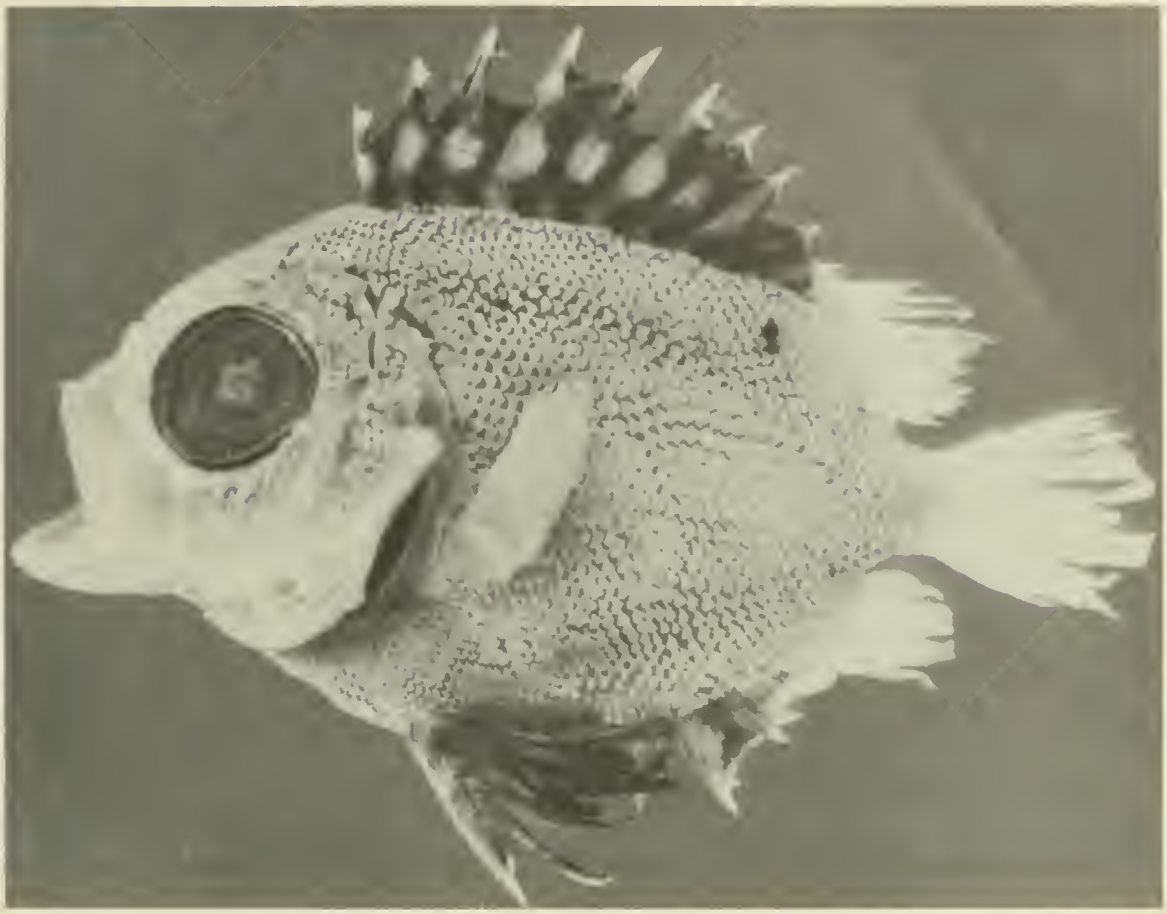

FIGURE 14.—Pelagic prejuvenile *Pseudopriacanthus altus*, 19.9 mm. standard length (WHOI).

By 2.4 mm., a single series of closely arranged chromatophores had developed along the ventral midline of the postanal region, and very light pigmentation had appeared at the angle of the preopercle.

By 2.6 mm., pigmentation on the preopercle had spread to cover the basal two-thirds of the spine at the angle. In addition, pigment seemingly on the dorsal surface of the gut had intensified very noticeably and had begun to spread down over the sides of the gut. A 2.7-mm. individual also had several dark spots along the edge of the isthmus, the gill arches were darkening, a patch of small chromatophores was evident at the point where the tubular and bulky parts of the gut join within the dorsal region of the body cavity, and a single large chromatophore was present at the anal opening. In a second 2.7-mm. specimen the patch of pigment at the junction of the two sections of the gut extended along the apparent dorsoposterior surface of the tubular gut nearly to the anus. In both of these 2.7-mm. specimens there was a general darkening of the body, although individual chromatophores were not evident. At 3.2 mm. (fig. 9), a few small pigment spots were present on the caudal finfold. The chromatophores on the optic lobes or on the brain case had descended laterally.

The chromatophores on the optic lobes of the brain or on the brain case had descended farther by 3.9 mm., and the cleithrum had pigment along its inner edge—the only changes since 3.2 mm. By 4.0 mm., the spots on the developing caudal fin and those on the ventral midline had disappeared. In addition there was loss of some pigmentation on the preopercle, cleithrum, and gill arch. This loss was complete at 6.6 mm., except on the base of the preopercle-angle spine (fig. 10).

Other than a general darkening of the entire outer surface, which obscured the internal pigmentation, no further changes were noted until

FIGURE 15.—Pelagic prejuvenile *Pseudopriacanthus altus*, 34.0 mm. standard length (CU 27831).

8.2 mm., when small, very dark chromatophores were evident over most of the head and body. At 10.2 mm. these chromatophores had darkened the entire external surface. In addition, a series of many sharply defined dark spots had appeared on the future course of the lateral line. Above this series was a second row of about 10 evenly spaced, larger dots (these were still evident at 48.6 mm.; see fig. 17). No further changes in body pigment occurred by 15.0 mm. except for the reappearance of isolated dark spots in the region of the cleithrum (fig. 12). This color pattern persisted from about 20 to 30 mm., with the exception of a lightening of the skin and scales covering the bases of the caudal rays. At this approximate size, dark chromatophores began to outline the scales just anterior to their ctenii and to cover the scale pockets (see fig. 15). By 58.9 mm., the dark chromatophores covered only the pockets and gave the scales the appearance of having dark centers (fig. 18). Suggestions of three or four wide, poorly defined, incomplete vertical bars also appeared on the 34.0-mm. specimen illustrated in figure 15. These bars may persist to adulthood and are especially noticeable when the fish is alive. The chromatophores appearing over the center of those scales in the regions of the bars were more expanded and intense. This pigmentation persisted, especially above the lateral line, to the largest specimens.

Fin Pigmentation

Pectoral fins.—Immaculate at all sizes.

Pelvic fins.—All specimens up to 6.6 mm. had immaculate pelvic fins (figs. 8–10). By 8.2 mm., these fins had a scattering of small dark chromatophores along the rays and onto the membranes connecting them. These chromatophores spread and increased in number until the fins, with the exception of their immaculate tips, were completely covered with dark pigment by 10.2 mm. The tips also were covered by 15.0 mm. (fig. 12). In specimens larger than 10.2 mm., the pigment was progressively less intense on the rays than on

FIGURE 16.—Bottom-living prejuvenile *Pseudopriacanthus altus*, 40.7 mm. standard length (BLBG).

FIGURE 17.—Bottom-living prejuvenile *Pseudopriacanthus altus*, 48.6 mm. standard length (BLBG, *Silver Bay* 1299).

FIGURE 18.—Bottom-living prejuvenile *Pseudopriacanthus altus*, 58.9 mm. standard length (BLBG, *Silver Bay* 1268).

the membranes, until about 65 mm. (see fig. 19, 67.3 mm.) when, in the pigmented parts of the fin, it was concentrated almost entirely on the membranes. This pigmentation persisted through the largest sizes.

During the above sequence, beginning in a 16.8-mm. specimen (fig. 13), the basal parts of these fins began to lose pigment, although it persisted here in some specimens to about 50 mm. (see fig. 17, 48.6 mm.). Loss of pigment progressed distally (figs. 18 through 22) until in the largest examples (fig. 23, 261.8 mm.), only dark tips remained, with streaks of less intense pigment along the inner edges of some soft-rays. In the adults, the rays nearest the spine were the most heavily pigmented, and the rays became progressively less pigmented away from the spine.

In some specimens as small as 12.8 mm., the pigment on the single spine formed a pattern of three or four bars across the spine. After about 19.9 mm. (fig. 14), all specimens up to about 75 mm. (figs. 15 through 19) had this pattern. It was most intense at about 50 mm., and gradually diminished until the spine became immaculate after about 75 mm.

Caudal fin.—All specimens up to about 19.9 mm. (figs. 8–14) had immaculate caudal fins. A 22.9-mm. specimen also appeared to have an immaculate fin—a part of the fin was missing. A 23.2-mm. specimen bore small dark specks arranged in several irregular vertical rows along the caudal rays. This pigment pattern persisted until metamorphosis had begun. Unmetamorphosed specimens as large as 57.1 mm. showed this coloration, and one of them, 40.7 mm., is illustrated in figure 16. During metamorphosis (seen in specimens 34.5 to 65.2 mm.) the fin was specked, and the tips of the rays were nonpigmented. As metamorphosis progressed, these specks appeared to migrate distally along the rays and accumulate near the border of the fin, forming a band of black of varied intensity proximal to the light tips (figs. 16, 17, and 18). After metamorphosis was complete (in some specimens as small as 63.2 mm.) the fin was again immaculate except for the dark band, which from this stage onward appeared as a border on the fin (figs. 19 through 23).

FIGURE 19.—Juvenile *Pseudopriacanthus altus*, 67.3 mm. standard length (UF 1434).

Dorsal fin.—The dorsal fin was immaculate in specimens up to 5.3 mm. The soft part of this fin continued immaculate in specimens up to 12.1 mm. (fig. 11) and in some to as large as 16.5 mm.

The interspinous membranes received pigment the earliest, and this was first noted in a 6.6-mm. specimen (fig. 10). The numerous pigment spots occupied the middle half of the membranes connecting the first seven spines of the fin. At 8.2 mm. pigment was present over the entire spinous fin, with the exception of the tips.[2] This pigment pattern intensified, especially along the edges of the spines, until in a 10.2-mm. specimen the fin appeared very dark.

In a 12.1-mm. individual, unpigmented disk-shaped areas had begun to form on the spines and adjacent membranes, half on spine and half on membrane, about midway of each spine (fig. 11). These clear areas, seemingly formed by the migration of pigment, formed a row of spots parallel to the base of the fin. The pigmented edges of these light spots were darker than the adjacent membrane, probably due to the migration and consequent crowding of the pigment as it retreated to form the unpigmented area. Also at about 12 mm. pigment had begun to appear at, and adjacent to, the base of the soft part of the dorsal, covering progressively less of the posterior soft-rays and their membranes (fig. 11).

At 15.0 mm. (fig. 12), the unpigmented spots in the initial row on the spinous dorsal had become more prominent and a second series of spots had begun to form distally and parallel to them. The tips of the spines and membrane at the tips remained unpigmented. Also at 15.0 mm. single chromatophores had begun migrating along the soft rays (but not along the membranes) from the pigment at the base of the soft fin.

[2] In preserved material the clear tips of the interspinous membranes often were torn away, giving the impression of color extending to the edge of the fin—not to be confused with the apparently normal loss of the membranous flaps at the tips of the spines, which occurs with change of habitat, or at approximately 50–60 mm.

FIGURE 20.—Juvenile or adult *Pseudopriacanthus altus*, 108.3 mm. standard length (BLBG, *Oregon* 2608).

FIGURE 21.—Juvenile or adult *Pseudopriacanthus altus*, 129.8 mm. standard length (BLBG, *Silver Bay* 2079).

FIGURE 22.—Juvenile or adult *Pseudopriacanthus altus*, 236.6 mm. standard length (BLBG, *Silver Bay* 1393).

FIGURE 23.—Juvenile or adult *Pseudopriacanthus altus*, 261.8 mm. standard length (BLBG, *Silver Bay* 1393).

In a 16.8-mm. individual (fig. 13), a third row of light spots had begun to form at the base of the spinous dorsal, and pigment had just begun to form on the anteriormost inter-soft-ray membranes. This same dorsal-fin pigmentation was present in a 19.9-mm. individual (fig. 14).

By 34.0 mm. (fig. 15), three rows of unpigmented spots were prominent, and some of the spots extended anteriorly across the spine to the next interspinous membrane. A fourth row of spots had begun to form at the base of some spines. The pigment mass at the base of the rays and membranes of the soft dorsal fin had separated slightly from the base of the fin—a few isolated chromatophores remained on both the rays and their intermembranes. Scattered chromatophores were present on the soft-dorsal rays, between the pigment mass and the edge, forming several irregular rows parallel to the base of the fin. It seemed that a migrating chromatophore split upon reaching a branch in a soft-ray. In specimens of this size, about 34 mm., several light spots, similar to

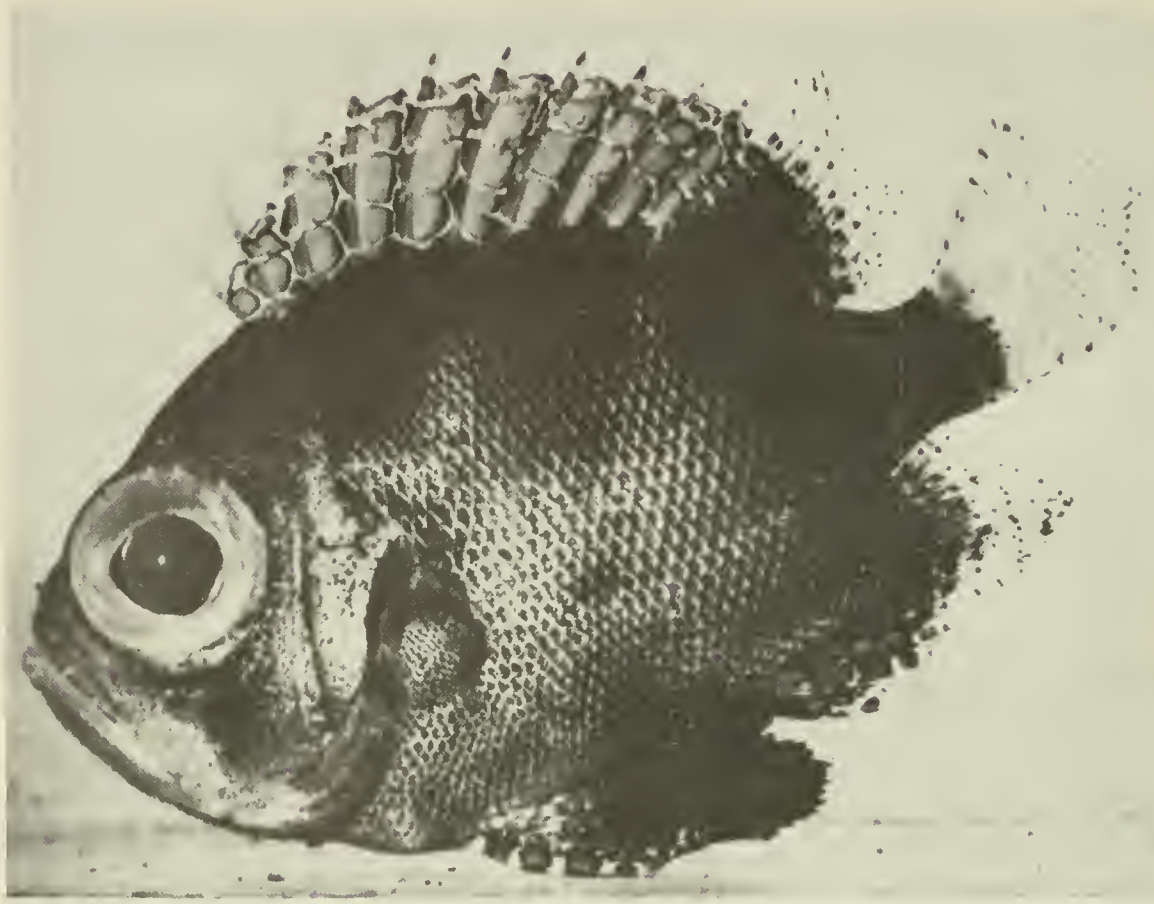

FIGURE 24.—Living prejuvenile *Pseudopriacanthus altus* (estimated 50 mm.).

those of the spinous part of the fin, were also present in the pigment mass at the base of the soft part of the fin.

On a 40.7-mm. specimen (fig. 16), the light spots on the spinous part of the dorsal fin had enlarged until there was only a suggestion of spots. The membrane bordering the anterior edge of each spine bore a line of dark pigment, and the spines retained a few chromatophores. The pigment mass near the base of the soft fin had moved farther distally, and the membranes were pigmented only at the base. The pigment mass was broken up by light spots. Distal to the mass, individual chromatophores were arranged in irregular rows, along the rays only, to the edge of the fin.

By 48.6 mm. (fig. 17), the spinous part of the fin was essentially unpigmented, except for a few scattered chromatophores near the anterior and posterior edges of the membranes. Some of the migrating pigment on the soft part of the fin had accumulated on the edge of the fin, particularly at the ends of the most anterior rays, and the chromatophores near the tips of the rays had broken into a mass of smaller spots extending onto the adjacent membranes. Of the original pigment mass at the base of the soft fin, only scattered chromatophores remained on the membranes and bands of pigment on the rays. In the basal area of the fin only the membranes retained pigment.

In a 58.9-mm. specimen (fig. 18) the lines of pigment on the membranes, parallel to the spines, were less intense, and all traces of the light spots on the spinous fin were gone. Some pigment remained at the distal edge of the interspinous membranes, especially on the most posterior spines, connecting the spines with a thin dark line. The basal half of the soft fin was immaculate and only a few scattered migrating chromatophores remained proximal to the dark anterior edge. The chromatophores on the posterior edge of the fin had nearly disappeared.

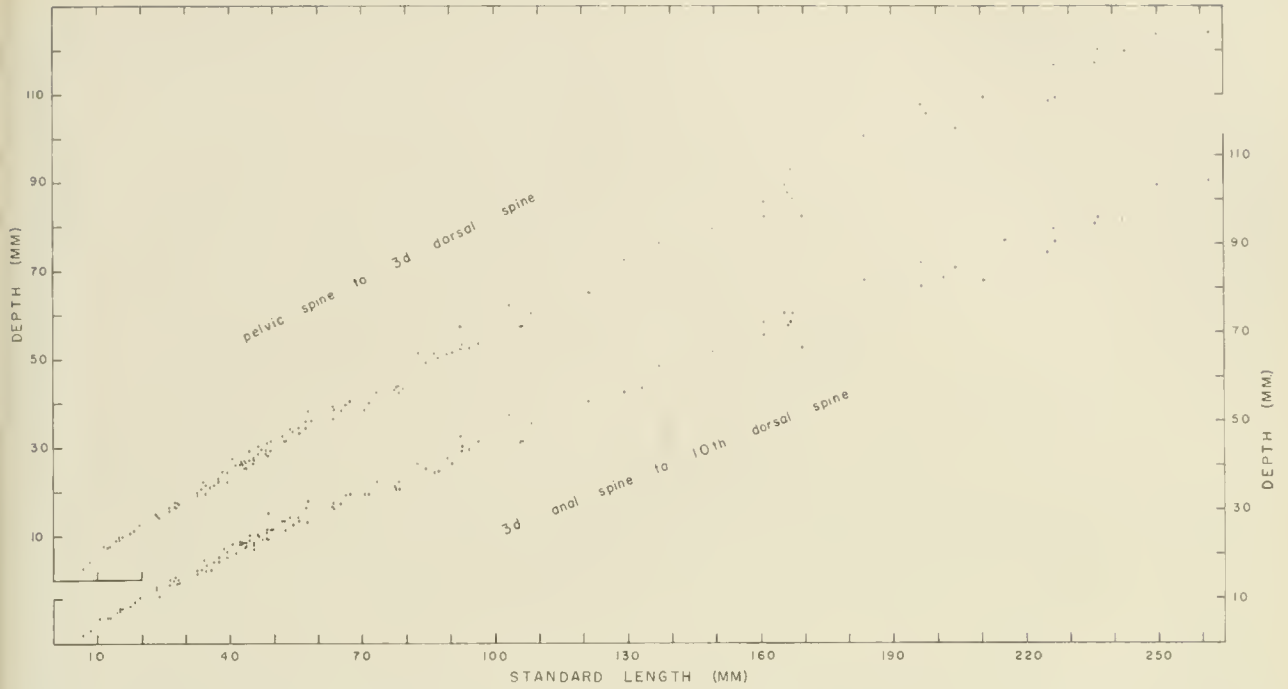

FIGURE 25.—Relation of body depth from pelvic spine insertion to 3d dorsal spine base and of body depth from 3d anal spine base to 10th dorsal spine base to standard length in *Pseudopriacanthus altus.*

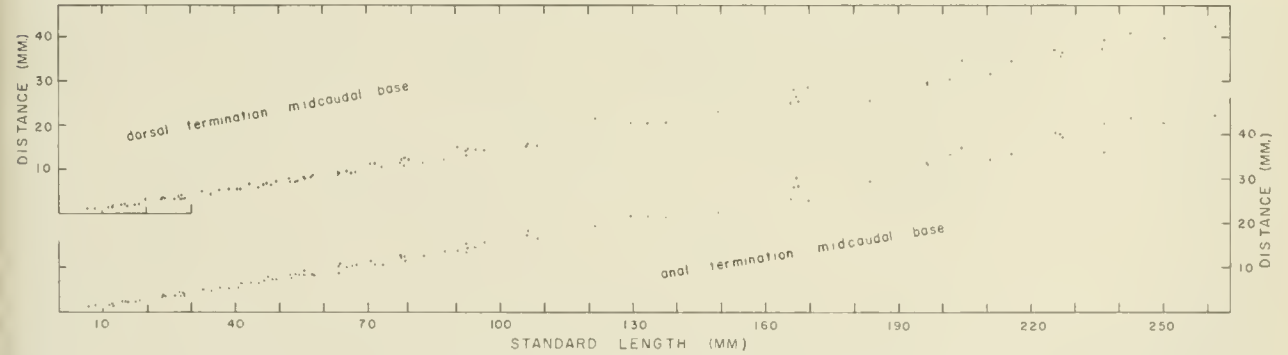

FIGURE 26.—Relation of distance from dorsal- and from anal-fin terminations to midcaudal base to standard length in *Pseudopriacanthus altus.*

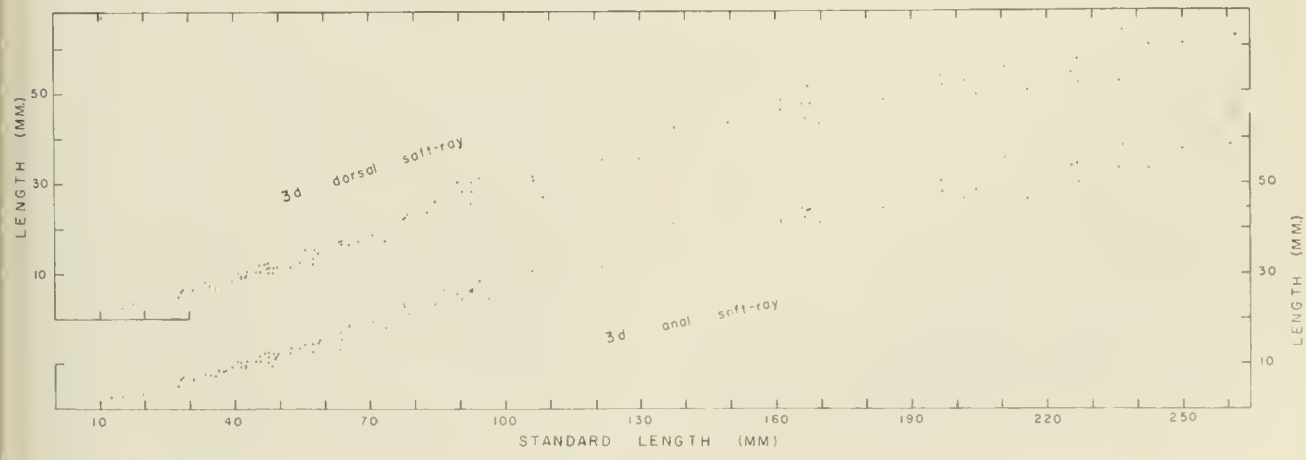

FIGURE 27.—Relation of lengths of 3d dorsal and 3d anal soft-ray to standard length in *Pseudopriacanthus altus.*

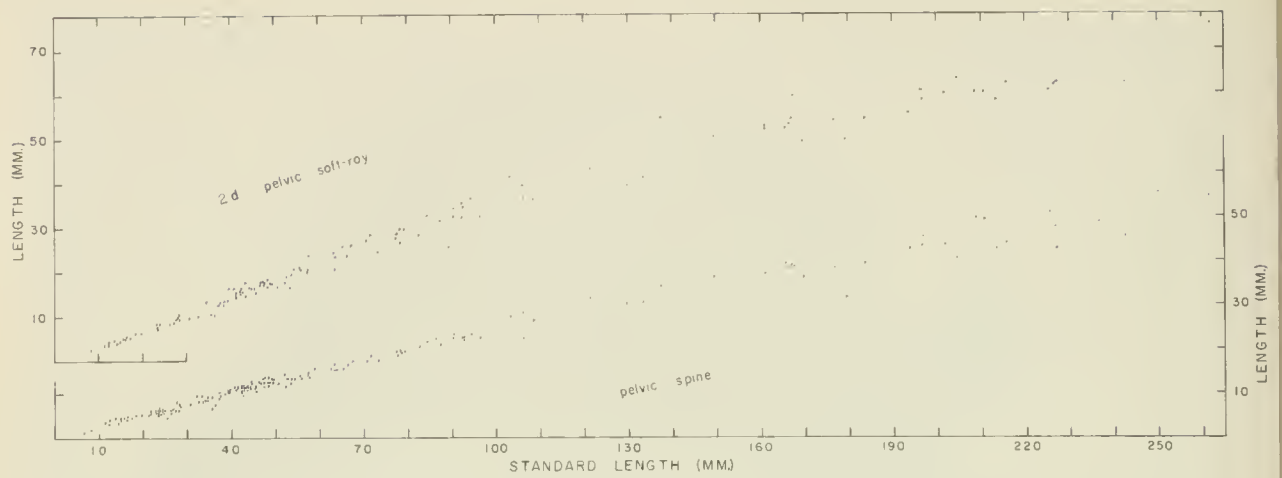

FIGURE 28.—Relation of length of pelvic spine and of 2d pelvic soft-ray to standard length in *Pseudopriacanthus altus*.

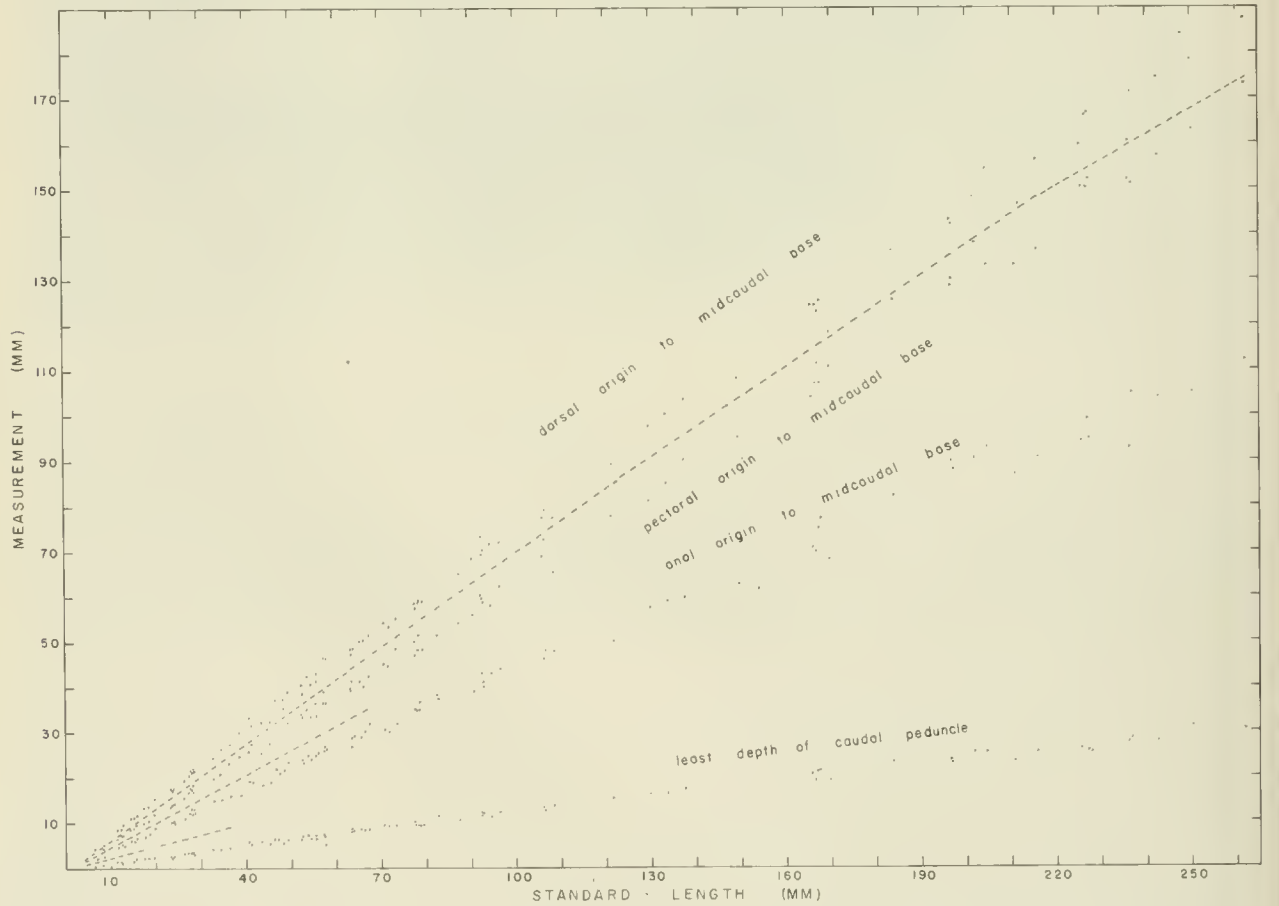

FIGURE 29.—Relation of least depth of caudal peduncle, of distance from origin of dorsal fin and from anal fin to midcaudal base, and of distance from origin of pectoral fin to midcaudal base to standard length in *Pseudopriacanthus altus*. (Dashed lines serve as guides in the separation of series of dots.)

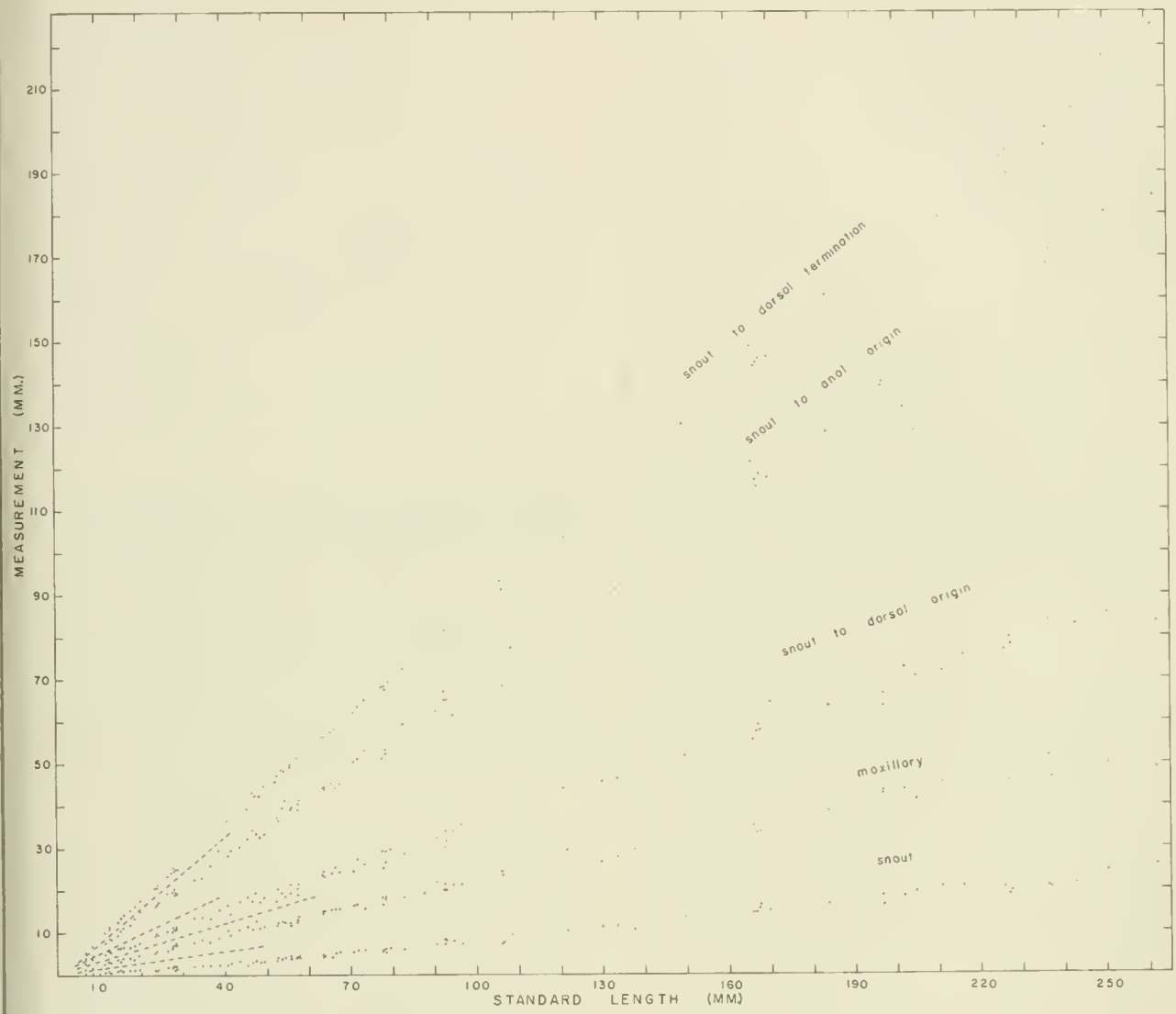

FIGURE 30.—Relation of snout length, of maxillary length, of distance from tip of snout to origins of dorsal and anal fins, and of distance from tip of snout to dorsal-fin termination to standard length in *Pseudopriacanthus altus*. (Dashed lines serve as guides in the separation of series of dots.)

In a 67.3-mm. individual (fig. 19), pigment of the dorsal fin consisted of only the black tips of the anteriormost soft-rays and traces of the lines parallel to the spines. In larger individuals, through the largest (261.8 mm.; see fig. 23), the lines of pigment parallel to the spines persisted in ever lessening degrees of intensity. The dark edge of the soft fin persisted without loss of intensity, and was broadest on the most anterior rays; it was never observed on the tips of the one or two most posterior soft-rays.

Anal fin.—The pigment pattern and its development on the anal fin were so similar to those of the dorsal fin, both in sequence and in size of fish at which the pattern developed, that it is unnecessary repetition to describe them here, other than to note a few minor differences.

Pigment on the anal fin was first observed on an 8.2-mm. specimen. Two rows of light spots, plus the light tips, appeared to be the maximum development of this pattern on the spinous fin, as seen at 34.0 mm. (similar to the maximum spotting on the spinous dorsal fin; see fig. 15). Lines of pigment parallel to the spines developed subsequent to the spots. The line anterior to the second spine persisted to about 65 mm., whereas

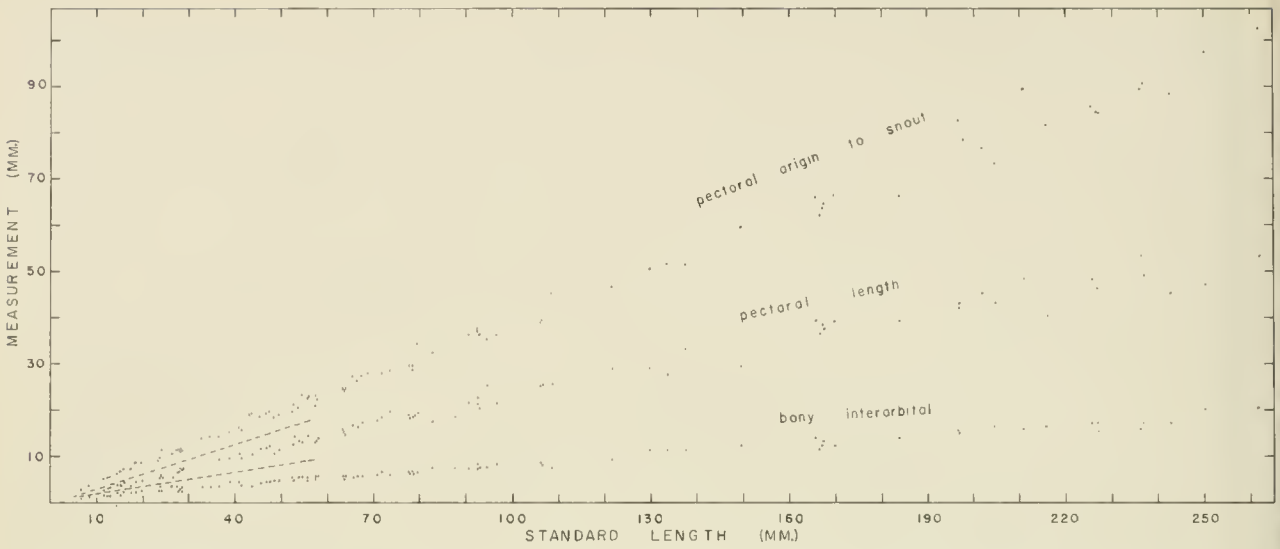

FIGURE 31.—Relation of interorbital width, of pectoral-fin length, and of distance from pectoral-fin origin to tip of snout to standard length in *Pseudopriacanthus altus*. (Dashed lines serve as guides in the separation of series of dots.)

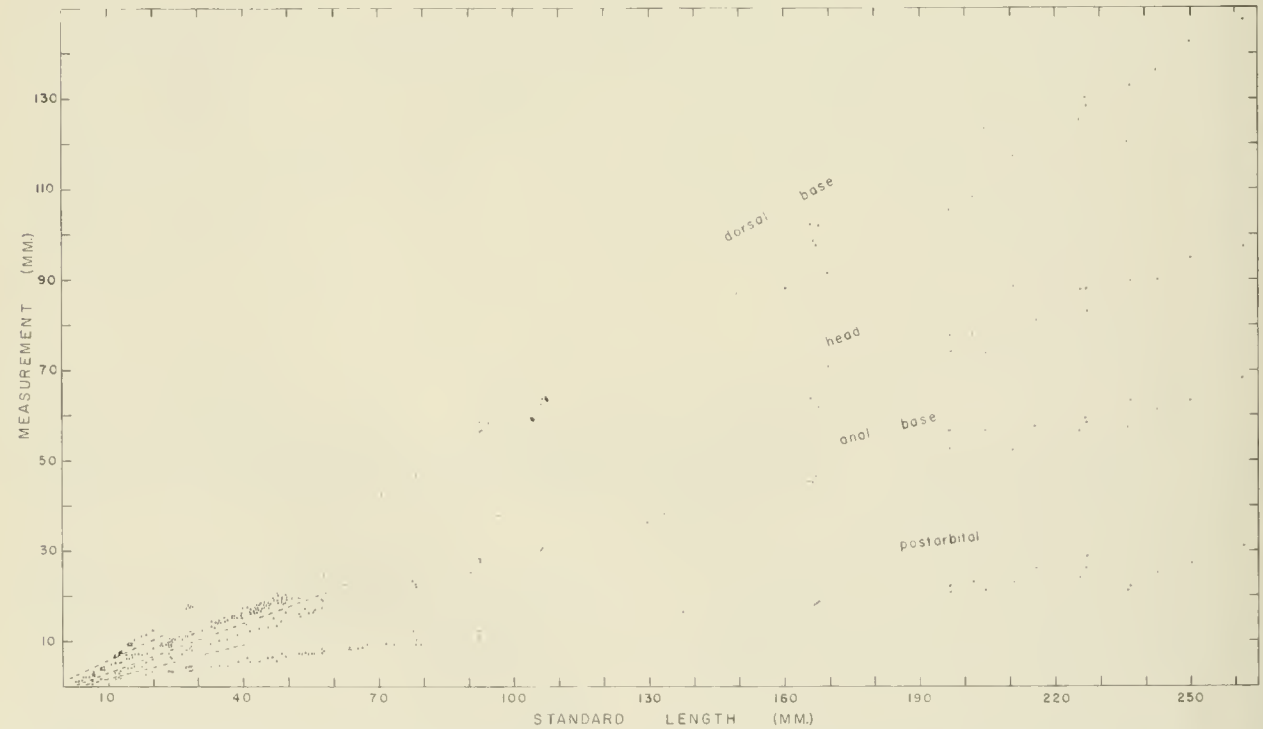

FIGURE 32.—Relation of postorbital length, of dorsal-fin and of anal-fin bases, and of head length to standard length in *Pseudopriacanthus altus*. (Dashed lines serve as guides in the separation of series of dots.)

the line adjacent to the third spine persisted to the largest size.

PIGMENTATION OF LIVING AND FRESHLY PRESERVED SPECIMENS

The following color notes were made on a 196.5-mm. specimen of *P. altus* collected by handline in 25 fathoms off Panama City, Florida, on April 19, 1958. The notes on live color were made from the fish just before preservation and from a Kodachrome transparency made of the specimen before preservation. The notes after preservation were made on April 21, after the fish had been killed and preserved in 10-percent formalin and not exposed to light beyond the first few hours.

In Life

Alive, and just after capture, the specimen was bright carmine with the exception of the black edges on the soft-dorsal and anal fins, and on the caudal and pelvic fins.

When the live fish was handled before preservation, its color faded into carmine bars and very light pink interspaces (see body pigmentation of preserved adult). The dorsal fin was yellow-orange below milky white tips. The iris of the eye was golden, and the surrounding areas carmine.

Two Days After Preservation

The interspinous membranes of the dorsal and anal fins were yellow except for milky areas in the shape of right triangles near the spine tips. The base of the triangle was parallel to the body of the fish, and the perpendicular side was against the anterior of the two spines. The leading edges of the dorsal spines were dark carmine except for their tips. The caudal, soft-dorsal, and soft-anal fins were light, mottled carmine with black edges. In the soft dorsal these mottled areas formed four alternating light and dark bands directed obliquely dorsoventrally, beginning with a dark anterior band. The pelvic fin was light carmine with a black edge, and the pectoral was light carmine.

These descriptions agree with the usual descriptions of color in the literature; i.e., a crimson fish with black markings on vertical and pelvic fins. The pattern of black, as noted in the description of preserved color, varies with the size of the fish. The brief color descriptions by Smith (1907: p. 285) and Jordan and Evermann (1896: p. 1240) apparently are from a large fish; that of Hildebrand and Schroeder (1928: p. 255) from a transforming prejuvenile.

The color of the live pelagic prejuvenile has not been described. That of a close relative, *Priacanthus cruentatus* (Lacépède), has been described elsewhere (D. K. Caldwell, in press) and consisted of blues and silvers—as expected in most pelagic prejuveniles (Hubbs, 1941: p. 184). The coloration of pelagic *Pseudopriacanthus altus* may be similar, with the red hue assumed almost immediately on arrival inshore.

The usual reference to color of specimens caught in tidepools—all such references seen were from the northern latitudes—is "bright red" (see for example, Nichols and Breder, 1927: p. 83). Scattergood and Coffin (1957: p. 156), in a more detailed description, said of the color of a 28-mm. individual collected in a trap set at 10 fathoms—

> The body color in life was orange red; the spiny dorsal fin had two rows of orange spots, two on each spine; the ventral spine had two orange spots; the iris had four white spots; and immediately above the lateral line was a row of 12 black blotches.

The lateral-line spots of my prejuvenile *Pseudopriacanthus altus* were discussed in the section on body pigmentation of preserved specimens. The orange spots on the spinous dorsal of Scattergood and Coffin's specimen apparently are the light spots I described for preserved specimens.

These spots on the spinous dorsal do appear dark in a black and white photograph of a living specimen of unstated size (fig. 24), taken through an aquarium glass at Marine Studios, Florida; I did not see the living fish. This fish is probably the same metamorphosing specimen I referred to earlier as being about 40 mm. at capture and 73 mm. at death. The date of capture was August 7, and that on the photograph, "Sept." In the photograph of the living fish the dark areas on the spinous fin are edged with black, as are the light areas on the same fin after preservation. The spaces between these black-edged disks are light on the living fish, while in a preserved specimen of slightly smaller size they are dusky (fig. 15). The spots Scattergood and Coffin referred to on the ventral spine are probably the light areas I referred to on the pelvic spine. Gordon (1960: plate 49) showed a photograph of an apparently freshly killed pretransformation prejuvenile exhibiting coloration similar to that of this living specimen. He described the color of the specimen

as brilliant red (p. 61). However, he indicated the specimen was collected inshore. A color transformation from blue-silver hues to red may be very rapid with change of habitat.

P. altus lives primarily in deeper water in dark crevasses of rocks. As pinks and reds become invisible in deep water, the short bigeye may possibly take on this coloration as camouflage. Dr. John E. Randall, first in conversation with Jack W. Gehringer in June 1960, and later by letter dated September 16, 1960, stated that closely related *Priacanthus arenatus* Cuvier seen just off the bottom in 60 feet of water on a reef at St. John, Virgin Islands, appeared a neutral gray to the eye and in a color motion picture film. Randall stated that on transport to the surface, the fish was a deep red, but that this change was an artifact of the loss of the red end of the spectrum at 60 feet and that a flash photograph of the fish at that depth in reality shows them to be dark red at all times.

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APPENDIX

The measurements taken which were only discussed and graphed, but otherwise not indicated by empirical values, are of considerable value to systematists, and have been included here in table A–1. Those measurements discussed in some degree are also included for completeness.

TABLE A–1.—*Empirical measurements (mm.) of selected body parts for 248 specimens of* Pseudopriacanthus altus *from throughout its range*

[See Definitions, p. 104 for method of taking measurement]

Body part measured	Standard length (mm.) of specimen																	
	2.2	2.4	2.6	2.7	2.7	3.2	3.2	3.4	3.5	3.9	4.0	4.4	4.8	5.2	5.3	5.8	6.6	8.2
Depth from pelvic spine base to 3d dorsal spine base																	2.8	4.1
Depth from 3d anal spine base to 10th dorsal spine base																	1.9	3.0
Head length				1.2		1.2	1.3			1.7	1.8	2.1	2.1		2.3		3.2	4.1
Snout–dorsal-fin origin																	2.9	3.9
Snout–dorsal-fin termination																	5.1	6.9
Snout–anal-fin origin																	4.1	4.7
Snout length																	0.7	0.7
Postorbital length																	0.8	1.6
Least depth of caudal peduncle																	0.7	0.9
Dorsal-fin origin–midcaudal base																	3.8	5.1
Dorsal-fin termination–midcaudal base																	1.1	1.1
Anal-fin origin–midcaudal base																	2.4	2.9
Anal-fin termination–midcaudal base																	1.1	1.3
Dorsal-fin base																	2.8	4.0
Anal-fin base																	1.2	1.9
Pectoral-fin origin–snout																	2.9	3.8
Pectoral-fin origin–midcaudal base																	3.3	4.1
Pectoral-fin length																		
Pelvic-spine length																	1.1	2.0
2d pelvic ray length																		2.5
Eye diameter	0.3	0.3	0.4	0.4	0.5	0.6	0.5	0.6	0.5	0.7	1.0	0.8	1.0	1.1	1.0	1.4	1.3	1.6
Interorbital width																	0.8	1.2
Maxillary length																	1.2	1.6
3d dorsal ray length																		
3d anal ray length																		

Body part measured	Standard length (mm.) of specimen																
	8.3	8.6	8.7	10.2	10.5	11.2	11.3	12.1	12.4	12.8	12.8	13.7	13.8	13.9	14.2	14.3	14.5	14.8
Depth from pelvic spine base to 3d dorsal spine base							7.4	7.7	7.8						9.0			
Depth from 3d anal spine base to 10th dorsal spine base							5.6	5.8	5.9						7.0			
Head length	4.0	4.1	4.5	5.0			5.5	5.7	5.9	5.8			6.5	7.1	6.5			
Snout–dorsal-fin origin							5.0	5.8	5.9						6.4			
Snout–dorsal-fin termination							10.0	11.0	11.4						12.8			
Snout–anal-fin origin							7.7	8.7	8.6						9.5			
Snout length							1.0	1.1	0.8						1.1			
Postorbital length							2.0	2.1	2.0						2.2			
Least depth of caudal peduncle							1.7	1.6	1.6						2.0			
Dorsal-fin origin–midcaudal base							8.4	8.8	9.7						11.0			
Dorsal-fin termination–midcaudal base							1.5	1.8	2.0						2.0			
Anal-fin origin–midcaudal base							5.0	5.6	5.4						6.5			
Anal-fin termination–midcaudal base							1.7	1.9	1.8						2.1			
Dorsal-fin base							6.8	7.2	7.5						9.2			
Anal-fin base							3.4	3.3	3.6						4.2			
Pectoral-fin origin–snout							5.1	5.5	5.7						6.4			
Pectoral-fin origin–midcaudal base							6.5	7.0	7.0						8.5			
Pectoral-fin length							2.5	3.0	3.2						3.7			
Pelvic-spine length							3.4	3.3	4.2				4.6		3.3			
2d pelvic ray length							3.7	3.9	4.3				4.7		4.0			
Eye diameter	1.8	1.8	2.0	2.5	2.2	2.2	2.6	2.5	2.6	2.8	2.6	3.0	3.0	3.3	2.9	3.0	2.8	2.8
Interorbital width							1.8	1.5	1.5						2.0			
Maxillary length							2.7	3.0	3.0						3.4			
3d dorsal ray length								2.4										
3d anal ray length								2.6										

TABLE A–1.—*Empirical measurements (mm.) of selected body parts for 248 specimens of* Pseudopriacanthus altus *from throughout its range*—Continued

Body part measured	Standard length (mm.) of specimen																	
	14.9	15.0	15.0	15.1	15.1	15.6	15.7	15.8	16.1	16.1	16.4	16.5	16.8	16.9	16.9	17.1	17.3	18.4
Depth from pelvic spine base to 3d dorsal spine base	------	9.4	9.6	------	------	------	------	10.0	------	------	------	------	------	------	------	------	10.8	11.2
Depth from 3d anal spine base to 10th dorsal spine base	------	7.3	7.1	------	------	------	------	7.9	------	------	------	------	------	------	------	------	8.4	9.1
Head length	------	7.0	6.8	------	------	------	------	7.4	6.8	------	7.3	------	------	------	------	------	7.4	7.6
Snout-dorsal-fin origin	------	6.5	------	------	------	------	------	6.7	------	------	------	------	------	------	------	------	6.6	7.0
Snout-dorsal-fin termination	------	13.7	------	------	------	------	------	14.2	------	------	------	------	------	------	------	------	15.2	16.3
Snout-anal-fin origin	------	10.9	------	------	------	------	------	11.1	------	------	------	------	------	------	------	------	12.0	13.3
Snout length	------	1.5	------	------	------	------	------	1.3	------	------	------	------	------	------	------	------	1.3	1.4
Postorbital length	------	2.3	------	------	------	------	------	2.6	------	------	------	------	------	------	------	------	2.6	2.9
Least depth of caudal peduncle	------	1.9	------	------	------	------	------	2.2	------	------	------	------	------	------	------	------	2.3	2.4
Dorsal-fin origin–midcaudal base	------	11.3	------	------	------	------	------	11.9	------	------	------	------	------	------	------	------	13.2	13.9
Dorsal-fin termination–midcaudal base	------	2.1	------	------	------	------	------	1.9	------	------	------	------	------	------	------	------	2.0	2.4
Anal-fin origin–midcaudal base	------	6.3	------	------	------	------	------	7.0	------	------	------	------	------	------	------	------	7.2	8.0
Anal-fin termination–midcaudal base	------	2.2	------	------	------	------	------	2.1	------	------	------	------	------	------	------	------	2.2	2.6
Dorsal-fin base	------	9.5	------	------	------	------	------	10.3	------	------	------	------	------	------	------	------	11.0	11.8
Anal-fin base	------	4.2	------	------	------	------	------	4.8	------	------	------	------	------	------	------	------	4.8	5.6
Pectoral-fin origin–snout	------	6.9	------	------	------	------	------	7.3	------	------	------	------	------	------	------	------	7.5	8.6
Pectoral-fin origin–midcaudal base	------	8.6	------	------	------	------	------	9.2	------	------	------	------	------	------	------	------	9.9	10.1
Pectoral-fin length	------	3.6	------	------	------	------	------	4.1	------	------	------	------	------	------	------	------	3.5	4.4
Pelvic-spine length	------	4.1	4.6	------	------	------	------	4.9	4.2	------	5.0	------	------	------	------	------	4.8	5.4
2d pelvic ray length	------	4.7	------	------	------	------	------	5.1	5.1	------	5.3	------	------	------	------	------	5.3	6.1
Eye diameter	3.4	3.1	3.2	2.9	3.0	3.0	3.2	3.0	3.0	3.1	3.5	3.0	3.4	3.4	3.6	3.4	3.5	3.6
Interorbital width	------	1.6	------	------	------	------	------	2.1	------	------	------	------	------	------	------	------	2.0	2.2
Maxillary length	------	3.1	------	------	------	------	------	4.0	------	------	------	------	------	------	------	------	4.0	3.9
3d dorsal ray length	------	2.8	------	------	------	------	------	------	------	------	------	------	------	------	------	------	3.6	------
3d anal ray length	------	2.7	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------

Body part measured	Standard length (mm.) of specimen																	
	18.4	19.9	19.9	21.1	21.7	21.8	22.9	23.2	23.3	23.5	23.5	23.5	23.5	23.6	23.7	23.8	23.9	24.0
Depth from pelvic spine base to 3d dorsal spine base	------	12.7	------	------	------	------	------	15.0	------	------	------	------	------	------	------	14.8	------	14.2
Depth from 3d anal spine base to 10th dorsal spine base	------	10.1	------	------	------	------	------	12.3	------	------	------	------	------	------	------	12.1	------	10.5
Head length	------	8.8	8.5	9.2	9.7	9.4	9.5	9.8	------	10.7	10.0	9.9	10.0	10.0	9.8	9.8	10.1	10.5
Snout-dorsal-fin origin	------	7.7	------	------	------	------	------	9.3	------	------	------	------	------	------	------	9.9	------	9.8
Snout-dorsal-fin termination	------	17.8	------	------	------	------	------	20.7	------	------	------	------	------	------	------	20.8	------	21.1
Snout-anal-fin origin	------	15.0	------	------	------	------	------	16.4	------	------	------	------	------	------	------	16.7	------	17.1
Snout length	------	1.7	------	------	------	------	------	1.7	------	------	------	------	------	------	------	1.4	------	1.6
Postorbital length	------	3.3	------	------	------	------	------	3.5	------	------	------	------	------	------	------	3.5	------	3.5
Least depth of caudal peduncle	------	2.4	------	------	------	------	------	2.9	------	------	------	------	------	------	------	2.9	------	2.9
Dorsal-fin origin–midcaudal base	------	15.3	------	------	------	------	------	17.9	------	------	------	------	------	------	------	17.4	------	17.3
Dorsal - fin termination–midcaudal base	------	3.3	------	------	------	------	------	3.2	------	------	------	------	------	------	------	3.7	------	3.6
Anal-fin origin–midcaudal base	------	9.4	------	------	------	------	------	10.6	------	------	------	------	------	------	------	10.8	------	10.1
Anal-fin termination–midcaudal base	------	3.3	------	------	------	------	------	3.4	------	------	------	------	------	------	------	3.6	------	3.7
Dorsal-fin base	------	12.4	------	------	------	------	------	15.4	------	------	------	------	------	------	------	14.9	------	13.8
Anal-fin base	------	6.2	------	------	------	------	------	7.5	------	------	------	------	------	------	------	6.9	------	6.6
Pectoral-fin origin–snout	------	8.7	------	------	------	------	------	9.2	------	------	------	------	------	------	------	9.9	------	11.2
Pectoral-fin origin–midcaudal base	------	11.6	------	------	------	------	------	13.4	------	------	------	------	------	------	------	13.8	------	14.0
Pectoral-fin length	------	4.6	------	------	------	------	------	5.1	------	------	------	------	------	------	------	5.8	------	5.2
Pelvic-spine length	------	5.3	------	5.4	5.7	6.1	6.3	6.4	------	5.1	5.9	6.3	6.0	5.7	6.6	5.8	15.8	5.8
2d pelvic ray length	------	6.1	------	------	------	------	------	8.4	------	7.3	------	------	------	------	------	7.2	------	8.4
Eye diameter	3.6	4.0	4.5	4.6	4.7	4.6	4.8	5.0	5.3	5.5	4.9	5.3	4.8	5.0	4.8	4.9	4.6	5.2
Interorbital width	------	2.7	------	------	------	------	------	2.9	------	------	------	------	------	------	------	3.2	------	2.6
Maxillary length	------	4.7	------	------	------	------	------	5.1	------	------	------	------	------	------	------	5.2	------	------
3d dorsal ray length	------	3.6	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------
3d anal ray length	------	3.3	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------	------

TABLE A–1.—*Empirical measurements (mm.) of selected body parts for 248 specimens of* Pseudopriacanthus altus *from throughout its range*—Continued

Body part measured	Standard length (mm.) of specimen																	
	24.1	24.2	24.4	24.5	25.0	25.6	26.1	26.4	26.6	27.4	27.9	28.0	28.1	28.4	30.8	32.7	32.8	33.2
Depth from pelvic spine base to 3d dorsal spine base							15.8	16.7		16.9	17.9	16.6	17.7	17.3		19.9	19.5	
Depth from 3d anal spine base to 10th dorsal spine base							13.2	14.5		14.1	14.8	13.8	14.1	13.9		16.3	15.6	
Head length	10.8	10.4	10.6	10.3	10.4	11.2	10.9	11.5	11.1	11.2	12.0	12.1	11.8	11.9	12.7	13.8	14.5	13.5
Snout–dorsal-fin origin							10.2			10.2	11.3	10.9	11.0	11.4			13.6	
Snout–dorsal-fin termination							23.3			24.1	25.4	24.6	25.0	25.0			29.7	
Snout–anal-fin origin							19.5			19.8	20.1	19.0	19.6	19.2			22.7	
Snout length							2.0			2.0	2.1	1.8	1.7	2.2			2.2	
Postorbital length							3.8			4.2	4.2	3.9	4.2	3.9			4.4	
Least depth of caudal peduncle							3.3			3.6	3.7	3.6	3.6	3.7			4.1	
Dorsal-fin origin–midcaudal base							19.5			20.6	21.8	21.8	22.0	21.5			24.5	
Dorsal-fin termination–midcaudal base							3.3			4.0	3.5	4.1	3.5	3.7			5.0	
Anal-fin origin–midcaudal base							11.2			12.8	13.3	12.5	13.1	12.6			15.1	
Anal-fin termination–midcaudal base							3.9			4.3	3.7	4.2	4.0	3.8			5.0	
Dorsal-fin base							16.4			17.1	18.0	17.5	17.9	17.9			20.0	
Anal-fin base							7.3			8.4	9.1	8.6	9.0	8.4			9.8	
Pectoral-fin origin–snout							10.6			11.5	11.5	11.4	11.3	11.6			14.0	
Pectoral-fin origin–midcaudal base							15.4			16.7	17.6	17.4	18.1	16.9			19.7	
Pectoral-fin length							5.5			6.5	6.9	7.1	7.1	7.0				
Pelvic-spine length	6.3	6.7	6.4	6.2	6.2	4.9	6.3	5.7	6.9	6.4	8.0	6.5	7.6	7.2	7.7	9.1	8.1	9.6
2d pelvic ray length							8.4			8.9	9.5	9.7	9.1	10.4	9.9		10.0	
Eye diameter	5.2	5.2	5.1	4.9	4.9	6.2	5.6	5.9	5.2	5.5	6.8	6.6	6.5	6.7	6.8	7.4	8.2	6.4
Interorbital width							3.2			3.4	2.4	2.8	2.2	3.1			3.1	
Maxillary length							5.8			6.1	6.9	7.0	7.0	7.4			7.9	
3d dorsal ray length										5.0		6.2		6.5	6.7		7.2	8.1
3d anal ray length										5.0		6.8		7.0	6.6			7.6

Body part measured	Standard length (mm.) of specimen																	
	33.9	34.0	34.5	34.8	35.7	35.7	36.4	37.1	37.3	37.5	37.6	38.4	38.8	39.2	39.2	39.2	39.9	40.7
Depth from pelvic spine base to 3d dorsal spine base	20.9	22.3	19.8	21.5		21.0	21.5		23.0	22.1			24.2	22.3	24.3			
Depth from 3d anal spine base to 10th dorsal spine base	16.9	18.8	16.4	17.7		16.7	18.1		18.3	19.3			21.2	19.4	20.5			
Head length	14.2	14.2	14.8	14.2	15.3	14.8	15.0	15.3	15.5	15.5	15.8	15.1	15.3	15.8	16.5	15.6	17.6	
Snout–dorsal-fin origin			13.7				13.3						15.2					
Snout–dorsal-fin termination			30.7				32.3						35.7					
Snout–anal-fin origin			23.0				26.0						29.3					
Snout length			2.6				2.7						2.6					
Postorbital length			4.8				4.7						5.4					
Least depth of caudal peduncle			4.2				4.8											
Dorsal-fin origin–midcaudal base			26.3				27.5						30.0					
Dorsal-fin termination–midcaudal base			4.5				5.4						5.5					
Anal-fin origin–midcaudal base			15.5				16.3						16.5					
Anal-fin termination–midcaudal base			4.9				5.4						5.1					
Dorsal-fin base			21.7				22.7						25.3					
Anal-fin base			10.4				10.8						11.7					
Pectoral-fin origin–snout			14.1				14.1						15.2					
Pectoral-fin origin–midcaudal base			20.7				23.0						24.6					
Pectoral-fin length							9.1						9.6					
Pelvic-spine length	8.2	8.6	8.7	9.3	6.7	9.2	7.5	10.2	9.0	10.2	9.8		10.0	10.3	10.3	10.6	11.0	
2d pelvic ray length			13.1		10.9		10.2	12.8			13.0	12.5	13.5			13.8		
Eye diameter	7.3	6.7	8.0	7.7	8.0	7.8	7.7	7.5	7.7	8.0	8.5	8.2	8.3	7.9	8.0	7.6	9.7	8.8
Interorbital width			3.3				3.5						4.2					
Maxillary length			8.1				7.9						8.9					
3d dorsal ray length			7.5		6.8		8.0	8.2			9.6					8.9		
3d anal ray length			7.7		7.3		8.7	8.2			8.4					9.1		

TABLE A–1.—*Empirical measurements (mm.) of selected body parts for 248 specimens of* Pseudopriacanthus altus *from throughout its range*—Continued

Body part measured	Standard length (mm.) of specimen																	
	40.9	41.1	41.1	41.1	42.1	42.2	42.4	42.4	42.6	42.7	42.9	42.9	43.4	43.5	43.6	43.7	44.2	44.4
Depth from pelvic spine base to 3d dorsal spine base	27.7	26.0	------	------	------	26.2	------	------	26.4	26.7	26.4	------	27.0	25.4	25.2	26.6	------	29.1
Depth from 3d anal spine base to 10th dorsal spine base	22.5	20.3	------	------	------	22.1	------	------	22.3	22.4	22.4	------	22.9	21.6	21.9	22.9	------	24.3
Head length	17.8	16.6	17.3	16.3	16.9	17.8	16.9	17.2	17.0	17.2	17.5	17.0	18.2	18.8	17.0	17.4	17.9	18.4
Snout–dorsal-fin origin	16.4	14.5	------	------	------	------	------	------	------	------	------	------	------	17.2	------	------	------	------
Snout–dorsal-fin termination	36.8	36.6	------	------	------	------	------	------	------	------	------	------	------	37.8	------	------	------	------
Snout–anal-fin origin	28.4	29.7	------	------	------	------	------	------	------	------	------	------	------	30.5	------	------	------	------
Snout length	2.7	3.0	------	------	------	------	------	------	------	------	------	------	------	3.5	------	------	------	------
Postorbital length	6.2	5.4	------	------	------	------	------	------	------	------	------	------	------	5.6	------	------	------	------
Least depth of caudal peduncle	6.0	5.1	------	------	------	------	------	------	------	------	------	------	------	6.0	------	------	------	------
Dorsal-fin origin–midcaudal base	33.2	31.8	------	------	------	------	------	------	------	------	------	------	------	32.3	------	------	------	------
Dorsal-fin termination–midcaudal base	5.6	5.8	------	------	------	------	------	------	------	------	------	------	------	6.9	------	------	------	------
Anal-fin origin–midcaudal base	19.8	19.1	------	------	------	------	------	------	------	------	------	------	------	18.8	------	------	------	------
Anal-fin termination–midcaudal base	5.6	6.4	------	------	------	------	------	------	------	------	------	------	------	6.6	------	------	------	------
Dorsal-fin base	28.2	26.2	------	------	------	------	------	------	------	------	------	------	------	26.1	------	------	------	------
Anal-fin base	14.2	12.5	------	------	------	------	------	------	------	------	------	------	------	13.0	------	------	------	------
Pectoral-fin origin–snout	16.1	15.8	------	------	------	------	------	------	------	------	------	------	------	19.2	------	------	------	------
Pectoral-fin origin–midcaudal base	25.6	27.2	------	------	------	------	------	------	------	------	------	------	------	25.2	------	------	------	------
Pectoral-fin length	10.7	9.7	------	------	------	------	------	------	------	------	------	------	------	10.4	------	------	------	------
Pelvic-spine length	11.7	11.1	11.5	11.2	11.1	10.3	10.7	11.6	10.9	11.4	9.6	11.9	11.6	10.9	11.4	11.8	11.7	11.3
2d pelvic ray length	16.4	14.6	14.9	15.4	15.6	------	15.4	16.1	------	------	------	15.7	17.7	14.6	------	------	16.5	------
Eye diameter	8.7	8.6	8.9	8.3	9.2	8.9	8.9	8.6	8.9	8.9	9.5	8.5	8.9	10.8	8.4	9.0	9.9	9.8
Interorbital width	4.1	3.9	------	------	------	------	------	------	------	------	------	------	------	3.5	------	------	------	------
Maxillary length	10.7	9.3	------	------	------	------	------	------	------	------	------	------	------	10.5	------	------	------	------
3d dorsal ray length	10.4	9.1	9.1	------	9.4	------	9.9	------	------	------	------	10.7	------	------	------	------	------	------
3d anal ray length	10.5	9.3	10.1	------	9.7	------	9.5	------	------	------	------	10.6	------	------	------	------	------	------

Body part measured	Standard length (mm.) of specimen																	
	44.6	44.9	45.2	45.5	45.5	45.6	46.5	46.6	47.1	47.2	47.2	47.3	48.2	48.3	48.4	48.6	49.0	49.3
Depth from pelvic spine base to 3d dorsal spine base	27.2	------	26.5	27.2	27.5	------	28.7	30.1	------	29.1	------	------	28.9	31.0	29.5	28.4	------	29.1
Depth from 3d anal spine base to 10th dorsal spine base	23.3	------	21.2	22.2	22.2	------	24.3	24.2	------	23.1	------	------	23.8	25.6	25.1	23.7	------	25.8
Head length	18.5	18.3	18.7	17.8	18.5	18.6	19.1	19.4	19.1	20.8	20.3	18.7	19.0	19.8	19.4	18.8	18.9	19.4
Snout–dorsal-fin origin	------	------	18.4	------	------	------	------	17.5	------	19.4	------	------	17.1	------	------	------	------	18.1
Snout–dorsal-fin termination	------	------	39.1	------	------	------	------	43.1	------	42.2	------	------	42.3	------	------	------	------	44.8
Snout–anal-fin origin	------	------	32.2	------	------	------	------	34.1	------	33.5	------	------	32.7	------	------	------	------	33.5
Snout length	------	------	2.8	------	------	------	------	3.2	------	3.6	------	------	3.4	------	------	------	------	3.5
Postorbital length	------	------	6.2	------	------	------	------	6.7	------	5.9	------	------	7.1	------	------	------	------	6.9
Least depth of caudal peduncle	------	------	5.8	------	------	------	------	6.1	------	6.5	------	------	5.9	------	------	------	------	6.4
Dorsal-fin origin–midcaudal base	------	------	32.6	------	------	------	------	37.2	------	35.2	------	------	37.5	------	------	------	------	39.0
Dorsal-fin termination–midcaudal base	------	------	6.0	------	------	------	------	6.7	------	6.8	------	------	6.7	------	------	------	------	7.3
Anal-fin origin–midcaudal base	------	------	19.4	------	------	------	------	22.4	------	21.3	------	------	22.0	------	------	------	------	23.8
Anal-fin termination–midcaudal base	------	------	6.4	------	------	------	------	7.0	------	7.9	------	------	7.3	------	------	------	------	7.2
Dorsal-fin base	------	------	26.5	------	------	------	------	30.4	------	29.2	------	------	30.7	------	------	------	------	32.8
Anal-fin base	------	------	13.1	------	------	------	------	15.3	------	13.7	------	------	14.6	------	------	------	------	16.8
Pectoral-fin origin–snout	------	------	18.7	------	------	------	------	19.4	------	19.8	------	------	18.3	------	------	------	------	19.0
Pectoral-fin origin–midcaudal base	------	------	27.3	------	------	------	------	30.6	------	28.0	------	------	31.6	------	------	------	------	32.0
Pectoral-fin length	------	------	11.7	------	------	10.5	------	11.8	------	12.2	------	------	10.5	------	------	------	------	11.2
Pelvic-spine length	12.7	12.4	------	11.6	11.3	12.6	12.6	12.4	13.6	11.7	12.4	13.6	12.9	11.8	13.9	12.8	13.1	12.7
2d pelvic ray length	------	16.3	16.3	------	------	15.3	------	17.0	17.7	17.5	17.5	17.8	16.8	18.1	------	------	17.8	17.4
Eye diameter	9.3	8.6	10.4	9.1	8.9	9.4	9.4	10.0	9.5	11.6	11.7	9.0	8.9	9.4	9.8	10.2	9.3	9.8
Interorbital width	------	------	4.0	------	------	------	------	4.5	------	4.7	------	------	4.7	------	------	------	------	4.8
Maxillary length	------	------	11.2	------	------	------	------	10.9	------	12.9	------	------	11.0	------	------	------	------	11.5
3d dorsal ray length	------	10.6	12.0	------	------	10.6	------	12.1	11.3	12.3	10.1	11.2	10.1	------	------	11.9	------	------
3d anal ray length	------	10.8	11.7	------	------	10.8	------	12.4	------	12.7	10.2	11.7	9.7	------	------	12.1	11.7	11.6

TABLE A-1.—*Empirical measurements (mm.) of selected body parts for 248 specimens of* Pseudopriacanthus altus *from throughout its range*—Continued

Body part measured	Standard length (mm.) of specimen																	
	49.3	49.4	50.8	52.0	52.3	52.6	53.5	53.9	54.3	55.6	55.9	57.1	57.3	57.9	58.9	62.5	63.2	63.4
Depth from pelvic spine base to 3d dorsal spine base	------	31.7	------	32.8	31.5	31.5	------	34.0	33.7	34.5	33.1	36.0	34.5	38.1	36.0	------	39.4	38.4
Depth from 3d anal spine base to 10th dorsal spine base	------	25.9	------	27.7	27.7	25.4	------	28.4	26.8	28.4	27.5	30.5	27.4	32.0	29.3	------	31.5	30.9
Head length	20.4	19.6	19.7	19.8	19.8	22.6	19.9	21.8	22.3	22.8	22.1	22.3	22.2	24.1	23.3	24.8	26.3	26.4
Snout-dorsal-fin origin	------	------	------	------	17.6	20.2	------	19.3	18.6	21.4	19.3	20.3	19.0	21.7	------	------	23.7	24.2
Snout-dorsal-fin termination	------	------	------	------	45.8	47.2	------	48.7	48.4	49.2	49.2	51.5	50.7	52.8	------	------	55.8	56.3
Snout-anal-fin origin	------	------	------	------	37.1	36.8	------	39.9	41.2	39.4	39.6	39.2	40.9	41.2	------	------	44.4	44.6
Snout length	------	------	------	------	3.9	4.2	------	4.0	4.1	4.9	4.2	4.4	4.2	4.5	------	------	5.0	4.9
Postorbital length	------	------	------	------	7.3	7.1	------	7.5	7.3	7.5	7.5	8.4	7.9	8.0	------	------	8.3	8.6
Least depth of caudal peduncle	------	------	------	------	6.6	7.0	------	7.1	6.8	7.1	6.8	7.7	7.1	8.3	------	------	8.3	8.9
Dorsal-fin origin–midcaudal base	------	------	------	------	40.8	38.8	------	42.5	40.7	41.5	43.0	46.6	45.1	46.5	------	------	48.9	47.3
Dorsal-fin termination–midcaudal base	------	------	------	------	8.0	7.1	------	7.1	7.6	8.1	8.0	8.3	8.1	8.8	------	------	8.9	9.5
Anal-fin origin–midcaudal base	------	------	------	------	24.3	23.8	------	25.4	24.1	25.7	25.9	27.2	26.1	26.7	------	------	29.4	27.1
Anal-fin termination–midcaudal base	------	------	------	------	8.2	7.6	------	8.3	8.3	9.1	8.1	8.5	8.7	8.6	------	------	10.2	8.8
Dorsal-fin base	------	------	------	------	33.4	32.0	------	35.6	33.3	34.2	35.5	38.6	37.6	38.7	------	------	40.6	39.2
Anal-fin base	------	------	------	------	16.1	15.8	------	17.3	16.5	16.9	17.0	19.5	17.8	19.0	------	------	18.7	19.2
Pectoral-fin origin–snout	------	------	------	------	19.6	21.2	------	20.6	23.2	22.7	22.9	21.0	23.1	22.2	------	------	24.8	24.6
Pectoral-fin origin–midcaudal base	------	------	------	------	34.0	33.1	------	35.0	33.3	36.1	33.8	39.0	36.5	36.5	------	------	39.8	39.6
Pectoral-fin length	------	------	------	------	12.3	14.1	------	13.3	13.0	14.4	------	13.2	13.0	13.9	------	------	15.7	15.6
Pelvic-spine length	13.3	13.2	12.1	14.4	11.6	13.5	12.2	13.2	13.2	14.0	13.6	14.6	14.8	13.6	15.6	15.8	16.8	15.4
2d pelvic ray length	------	------	16.8	------	17.9	19.0	16.5	19.7	20.4	21.0	20.6	20.0	20.1	23.8	------	------	24.3	23.3
Eye diameter	9.8	9.9	9.9	10.0	10.5	12.3	10.6	10.7	11.2	12.5	10.3	10.6	10.5	12.0	12.0	12.7	14.0	14.0
Interorbital width	------	------	------	------	5.1	4.7	------	5.2	5.1	4.9	5.4	5.8	5.4	5.8	------	------	5.0	5.8
Maxillary length	------	------	------	------	11.6	12.3	------	12.6	12.3	12.3	11.8	13.0	12.8	13.8	------	------	15.0	14.7
3d dorsal ray length	------	11.9	------	------	11.9	14.7	------	------	12.7	15.3	------	13.7	12.3	15.7	14.8	------	17.1	17.0
3d anal ray length	------	12.0	------	------	12.4	13.7	------	------	13.7	14.4	------	14.7	12.8	14.9	15.0	------	18.1	17.0

Body part measured	Standard length (mm.) of specimen																	
	63.7	65.2	66.1	67.3	70.8	71.7	73.2	77.5	77.9	78.2	78.3	79.2	82.7	84.5	86.2	87.2	89.4	90.4
Depth from pelvic spine base to 3d dorsal spine base	36.4	38.1	39.8	40.5	38.9	40.0	42.8	43.3	43.9	44.0	42.3	43.5	51.9	49.1	51.1	50.5	51.2	51.6
Depth from 3d anal spine base to 10th dorsal spine base	30.4	31.5	33.1	33.6	33.8	33.7	36.1	35.3	34.8	36.2	34.8	------	40.4	39.2	38.4	38.9	41.7	40.5
Head length	26.3	27.3	27.7	27.9	29.6	28.8	27.8	30.2	33.5	30.4	29.7	32.1	33.2	35.3	35.8	35.2	37.8	34.8
Snout-dorsal-fin origin	23.1	24.0	25.7	24.2	24.6	27.3	26.2	29.1	25.1	26.6	29.1	29.8	28.6	------	------	------	------	32.6
Snout-dorsal-fin termination	56.1	57.8	58.2	58.7	62.1	63.6	65.0	68.2	------	68.0	67.9	69.5	72.5	------	------	------	------	78.9
Snout-anal-fin origin	44.3	45.8	44.3	45.2	50.9	51.2	53.4	51.3	------	52.6	53.7	------	59.8	------	------	------	------	62.7
Snout length	4.9	4.4	5.3	5.7	5.8	6.0	6.0	5.9	5.9	6.2	5.5	6.1	6.2	------	------	------	------	7.1
Postorbital length	8.3	8.6	8.9	9.4	9.6	9.9	9.1	8.8	12.4	10.1	9.1	9.4	10.4	------	------	------	------	10.2
Least depth of caudal peduncle	8.5	8.9	8.6	8.9	9.5	9.4	9.6	10.2	9.7	9.7	9.9	9.9	11.6	------	------	10.9	------	11.1
Dorsal-fin origin–midcaudal base	48.9	50.2	50.5	51.6	54.3	53.3	55.1	58.7	57.4	58.9	59.0	59.0	62.6	------	------	65.0	------	68.3
Dorsal-fin termination–midcaudal base	9.2	9.8	9.4	9.6	11.1	11.3	10.6	11.6	12.3	11.0	12.7	12.2	11.5	------	------	12.2	------	15.0
Anal-fin origin–midcaudal base	29.4	29.4	30.6	32.4	31.0	30.5	32.1	35.9	35.3	37.0	35.4	------	37.7	------	------	38.8	------	39.2
Anal-fin termination–midcaudal base	10.6	10.0	10.3	10.6	11.1	10.6	10.9	12.8	12.4	11.3	12.5	------	12.6	------	------	13.9	------	13.9
Dorsal-fin base	39.7	40.0	41.2	42.2	12.5	43.7	45.1	48.0	45.7	48.7	46.8	47.5	52.1	------	------	52.2	------	54.8
Anal-fin base	19.2	19.3	21.2	21.3	20.3	21.5	21.1	23.5	23.4	22.9	22.3	------	24.7	------	------	25.1	------	25.5
Pectoral-fin origin–snout	24.6	27.3	26.3	27.4	28.0	28.0	28.9	29.6	------	29.6	28.9	34.5	32.4	------	------	------	------	36.5
Pectoral-fin origin–midcaudal base	41.1	41.2	40.0	42.4	45.0	44.6	48.5	50.0	47.0	48.1	51.4	48.1	51.6	------	------	54.0	------	56.0
Pectoral-fin length	14.6	16.7	16.4	17.1	17.9	18.6	14.9	18.3	18.5	18.7	18.8	19.3	17.5	------	------	18.5	------	21.7
Pelvic-spine length	15.3	15.8	16.6	17.3	17.3	18.1	17.6	19.4	18.7	19.9	19.2	19.5	20.7	21.9	22.4	21.0	------	22.1
2d pelvic ray length	20.7	25.4	23.8	26.0	27.0	28.2	24.2	27.7	28.7	29.8	26.8	29.7	28.2	32.6	------	31.5	25.7	32.7
Eye diameter	14.0	15.1	14.6	14.5	15.7	15.0	15.6	17.0	16.4	17.4	16.3	18.9	16.6	17.8	20.5	17.1	21.0	19.3
Interorbital width	5.5	5.3	5.6	5.9	6.0	6.7	6.0	6.6	6.2	6.1	6.4	6.4	7.8	------	------	7.4	------	7.4
Maxillary length	15.0	15.5	15.5	15.6	16.5	------	15.6	18.1	16.9	18.2	17.7	------	18.4	19.5	------	19.1	------	22.0
3d dorsal ray length	16.3	16.7	------	17.1	18.8	------	17.5	22.1	22.5	23.1	17.3	------	23.7	26.0	27.9	26.6	30.4	28.3
3d anal ray length	15.2	18.6	------	19.2	19.4	------	18.0	23.1	22.6	21.9	21.3	------	23.0	23.3	26.5	23.2	25.7	24.4

TABLE A–1.—*Empirical measurements (mm.) of selected body parts for 248 specimens of* Pseudopriacanthus altus *from throughout its range*—Continued

Body part measured	Standard length (mm.) of specimen																	
	90.5	92.1	92.4	92.7	94.3	96.3	103.1	106.0	106.1	108.3	121.3	129.8	133.4	137.2	149.2	161.0	161.0	165.8
Depth from pelvic spine base to 3d dorsal spine base	------	57.4	52.1	53.2	52.8	53.7	62.1	57.1	57.4	60.3	65.0	72.6	69.2	76.4	79.8	82.4	85.9	89.5
Depth from 3d anal spine base to 10th dorsal spine base	------	46.6	43.1	44.4	43.8	45.8	51.4	45.2	45.3	49.3	54.5	56.6	57.2	62.4	65.8	69.1	72.4	74.1
Head length	------	36.6	35.7	36.1	37.2	37.5	40.7	41.5	40.5	45.7	49.3	50.9	51.0	52.3	58.1	59.3	62.2	63.6
Snout–dorsal-fin origin	------	34.0	30.1	31.6	34.0	35.9	------	41.2	37.8	40.0	44.0	45.9	46.1	47.5	51.9	------	------	55.1
Snout–dorsal-fin termination	------	82.7	81.0	81.1	81.3	84.0	------	93.4	91.2	95.5	103.7	112.1	116.9	120.2	130.1	------	------	148.6
Snout–anal-fin origin	------	65.1	67.4	65.1	61.7	65.4	------	73.5	68.7	77.6	83.8	88.1	91.4	96.1	107.8	------	------	121.5
Snout length	------	8.6	7.4	8.4	8.0	7.3	------	7.6	7.6	9.7	10.5	11.2	11.5	10.8	13.6	------	------	14.6
Postorbital length	------	12.0	11.0	10.9	11.8	12.0	------	12.2	12.9	12.8	14.5	15.5	15.2	16.7	17.5	------	------	20.6
Least deptb of caudal peduncle	------	12.2	11.9	12.0	11.9	12.4	------	13.1	12.8	13.9	15.2	16.1	16.5	17.6	19.3	------	------	20.7
Dorsal-fin origin–midcaudal base	------	73.1	69.4	70.1	71.8	72.0	------	77.8	79.2	77.5	89.4	97.9	100.3	103.8	108.1	------	------	124.5
Dorsal-fin termination–midcaudal base	------	14.1	13.1	14.6	14.4	14.3	------	15.3	15.7	15.5	21.5	20.6	20.6	20.8	23.0	------	------	25.0
Anal-fin origin–midcaudal base	------	43.4	40.5	41.6	43.5	44.5	------	46.9	48.7	48.3	50.6	58.0	59.6	60.3	63.2	------	------	71.1
Anal-fin termination–midcaudal base	------	15.2	13.3	14.4	14.8	15.8	------	17.1	18.1	16.8	19.2	21.7	21.5	21.3	22.5	------	------	25.3
Dorsal-fin base	------	58.8	56.6	56.5	58.2	58.7	------	62.5	63.9	62.1	70.2	78.8	81.2	83.6	87.0	------	------	102.2
Anal-fin base	------	28.5	28.3	27.6	29.5	28.4	------	30.2	30.6	31.1	31.4	36.5	38.4	38.9	40.5	------	------	45.4
Pectoral-fin origin–snout	------	37.2	37.6	36.3	35.4	36.3	------	39.0	39.8	45.2	46.9	50.6	51.6	51.5	59.8	------	------	66.0
Pectoral-fin origin–midcaudal base	------	60.2	59.7	58.7	58.0	62.2	------	69.0	72.8	65.1	78.0	81.2	85.1	90.3	95.3	------	------	104.2
Pectoral-fin length	------	22.8	21.1	20.2	25.3	21.8	------	25.2	25.2	25.9	29.0	29.0	27.8	33.1	29.7	------	------	39.2
Pelvic-spine length	23.1	22.8	22.9	22.0	23.2	22.7	27.6	28.1	22.9	26.2	31.5	30.1	30.6	34.1	36.2	35.1	37.0	39.1
2d pelvic ray length	34.2	32.2	35.3	34.3	36.8	32.5	41.5	39.3	36.8	36.3	43.2	39.5	41.2	54.9	50.4	52.8	52.0	52.3
Eye diameter	19.2	17.9	18.0	18.7	19.8	19.3	19.9	21.7	21.7	24.1	26.2	26.7	27.1	25.7	29.0	30.3	31.0	31.5
Interorbital width	------	8.3	7.2	7.3	7.6	8.4	------	8.7	8.0	7.8	9.3	11.1	11.1	11.4	12.5	------	------	14.4
Maxillary length	------	21.3	20.0	20.0	21.4	21.2	------	24.2	23.5	25.5	29.5	26.9	27.9	29.7	31.5	------	------	35.0
3d dorsal ray length	------	25.6	30.3	28.4	31.2	27.2	------	31.9	30.8	27.0	35.2	35.7	34.3	42.3	43.8	48.3	46.3	47.6
3d anal ray length	------	26.1	26.5	25.4	28.9	24.6	------	30.9	28.2	26.1	31.5	35.0	35.1	41.0	41.9	41.1	41.9	44.7

Body part measured	Standard length (mm.) of specimen																	
	166.5	167.0	167.5	169.9	176.9	179.2	179.3	182.1	183.6	190.9	193.8	195.3	196.5	196.9	198.9	201.7	204.3	208.6
Depth from pelvic spine base to 3d dorsal spine base	87.9	93.0	86.4	82.2	------	------	------	------	100.6	------	------	------	107.8	100.7	------	103.2	102.4	------
Depth from 3d anal spine base to 10th dorsal spine base	71.8	72.5	74.1	66.6	------	------	------	------	81.8	------	------	------	85.9	80.4	------	82.2	84.6	------
Head length	60.6	64.7	61.6	70.5	------	------	------	------	71.2	------	------	------	77.1	73.9	------	77.2	73.4	------
Snout–dorsal-fin origin	57.3	59.0	57.6	64.1	------	------	------	------	63.9	------	------	------	63.5	66.4	------	72.6	70.3	------
Snout–dorsal-fin termination	144.0	144.8	145.7	146.1	------	------	------	------	160.6	------	------	------	169.8	170.9	------	174.4	174.4	------
Snout–anal-fin origin	117.2	115.8	118.9	117.8	------	------	------	------	128.6	------	------	------	139.4	140.3	------	134.2	128.8	------
Snout length	14.6	15.3	16.2	15.0	------	------	------	------	16.5	------	------	------	18.5	16.4	------	18.3	19.1	------
Postorbital length	18.2	18.9	19.0	17.8	------	------	------	------	21.8	------	------	------	22.5	21.0	------	23.2	21.5	------
Least depth of caudal peduncle	19.1	21.1	21.5	19.4	------	------	------	------	23.2	------	------	------	23.6	23.2	------	25.1	25.1	------
Dorsal-fin origin–midcaudal base	124.5	123.0	125.4	118.5	------	------	------	------	136.4	------	------	------	143.1	142.1	------	148.2	154.5	------
Dorsal-fin termination–midcaudal base	28.0	26.7	25.4	28.9	------	------	------	------	25.7	------	------	------	29.6	29.7	------	30.4	34.7	------
Anal-fin origin–midcaudal base	70.3	75.5	72.9	68.7	------	------	------	------	82.6	------	------	------	90.3	88.7	------	91.0	93.2	------
Anal-fin termination–midcaudal base	28.0	30.1	28.4	25.0	------	------	------	------	29.5	------	------	------	33.8	33.3	------	35.9	37.0	------
Dorsal-fin base	98.9	97.8	102.0	91.4	------	------	------	------	111.4	------	------	------	115.5	114.2	------	118.4	123.2	------
Anal-fin base	45.2	46.6	45.0	39.8	------	------	------	------	52.6	------	------	------	56.7	52.7	------	55.1	56.7	------
Pectoral-fin origin–snout	62.0	63.9	64.6	66.5	------	------	------	------	66.2	------	------	------	82.7	78.2	------	76.7	73.1	------
Pectoral-fin origin–midcaudal base	107.2	111.9	107.5	111.0	------	------	------	------	125.9	------	------	------	128.9	130.3	------	138.2	133.5	------
Pectoral-fin length	36.8	38.6	37.8	39.1	------	------	------	------	39.1	------	------	------	42.1	43.2	------	45.5	43.5	------
Pelvic-spine length	38.4	39.0	38.8	36.2	38.2	39.6	31.8	39.2	39.4	41.6	42.6	45.0	43.3	45.4	42.0	43.6	40.6	49.8
2d pelvic ray length	53.3	54.5	59.7	49.1	54.0	56.2	49.7	60.5	54.2	54.5	55.9	62.7	60.8	58.7	54.2	60.0	63.4	60.2
Eye diameter	32.0	34.1	30.8	32.1	34.4	38.2	37.4	32.4	35.1	40.3	41.3	41.2	36.5	39.4	38.0	39.4	37.3	45.4
Interorbital width	11.9	12.6	13.2	12.2	------	------	------	------	14.0	------	------	------	15.7	15.3	------	16.5	16.8	------
Maxillary length	33.5	37.4	33.8	37.6	------	------	------	------	38.6	------	------	------	42.6	43.1	------	43.7	41.3	------
3d dorsal ray length	44.2	51.6	47.6	43.2	------	------	------	------	48.7	------	------	------	53.8	51.8	------	52.8	49.5	------
3d anal ray length	42.6	44.0	44.1	41.2	------	------	------	------	44.2	------	------	------	50.4	48.0	------	46.6	48.7	------

TABLE A–1.—*Empirical measurements (mm.) of selected body parts for 248 specimens of* Pseudopriacanthus altus *from throughout its range*—Continued

Body part measured	Standard length (mm.) of specimen																
	210.7	211.5	213.2	214.0	214.7	215.6	215.6	216.8	217.1	218.5	219.4	220.6	221.5	223.7	223.8	225.4	226.8	227.0
Depth from pelvic spine base to 3d dorsal spine base	109.1					106.5										108.7	116.7	109.5
Depth from 3d anal spine base to 10th dorsal spine base	81.8					90.9										88.0	93.5	90.7
Head length	88.0					80.8										87.4	87.1	82.8
Snout–dorsal-fin origin	71.8					75.2										76.5	79.5	77.7
Snout–dorsal-fin termination	179.5					185.7										193.8	195.2	189.8
Snout–anal-fin origin	156.9					149.7										158.9	159.3	158.6
Snout length	20.5					20.6										21.3	18.8	19.5
Postorbital length	23.1					26.2										24.7	26.4	29.0
Least depth of caudal peduncle	23.4					25.2										26.0	27.1	25.6
Dorsal-fin origin–midcaudal base	146.9					156.7										159.8	166.1	166.9
Dorsal-fin termination–midcaudal base	31.7					34.5										37.0	35.9	36.6
Anal-fin origin–midcaudal base	87.6					91.0										94.9	99.8	95.4
Anal-fin termination–midcaudal base	34.4					35.6										40.2	40.0	39.2
Dorsal-fin base	117.3					124.2										125.5	130.3	128.4
Anal-fin base	52.2					57.6										56.7	59.4	58.4
Pectoral-fin origin–snout	89.5					81.6										85.6	84.5	84.5
Pectoral-fin origin–midcaudal base	133.5					136.9										150.6	150.4	152.3
Pectoral-fin length	48.5					40.8										48.4	46.6	
Pelvic-spine length	49.2	43.2	42.8	44.6	47.3	44.0	46.5	45.5	45.4	43.9	43.6	45.0	43.3	46.0	47.3	51.0	47.8	42.9
2d pelvic ray length	60.2	60.6	58.6	60.4	66.9	62.3	62.4	62.7	60.7	59.2	63.1	62.4	58.8	63.1	62.1	60.9	62.0	62.1
Eye diameter	44.1	40.5	45.3	41.8	42.9	40.1	43.0	41.5	41.5	39.1	41.2	43.5	46.2	42.5	45.1	47.6	46.2	38.1
Interorbital width	16.0					16.8										17.1	17.4	15.7
Maxillary length	45.2					43.1										47.3	45.6	42.9
3d dorsal ray length	55.7					59.4										54.3	57.1	52.0
3d anal ray length	55.9					46.4										53.8	54.1	50.0

Body part measured	Standard length (mm.) of specimen													
	228.6	235.6	236.0	236.6	238.2	238.4	239.0	239.3	242.5	242.7	245.5	250.0	254.9	261.8
Depth from pelvic spine base to 3d dorsal spine base			117.4	120.3					119.9			123.8		124.0
Depth from 3d anal spine base to 10th dorsal spine base			94.6	96.0					95.6			103.2		104.4
Head length			85.0	89.0					89.4			94.3		96.7
Snout–dorsal-fin origin			83.8	81.1					82.8			85.4		83.0
Snout–dorsal-fin termination			196.4	200.2					205.0			217.8		225.0
Snout–anal-fin origin			168.3	161.9					165.7			180.6		184.8
Snout length			20.8	20.1					21.0			24.0		25.5
Postorbital length			21.7	27.5					25.3			27.5		31.2
Least depth of caudal peduncle			27.5	28.2					27.9			31.0		30.1
Dorsal-fin origin–midcaudal base			160.5	171.4					174.6			178.4		187.5
Dorsal-fin termination–midcaudal base			32.1	39.4					40.8			39.8		42.4
Anal-fin origin–midcaudal base			93.1	105.4					104.4			105.6		112.7
Anal-fin termination–midcaudal base			36.5	42.8					43.9			42.6		44.1
Dorsal-fin base			120.5	133.0					136.3			142.8		147.5
Anal-fin base			57.5	63.1					61.1			63.5		68.4
Pectoral-fin origin–snout			89.6	90.9					88.5			97.9		102.6
Pectoral-fin origin–midcaudal base			152.3	151.4					157.8			163.5		173.5
Pectoral-fin length			53.8	49.2					45.5			47.5		63.6
Pelvic-spine length	47.8	51.0	52.0	48.9	48.1	46.3	49.1	50.3	45.6	51.1	45.1	55.1	49.1	54.8
2d pelvic ray length	61.8	66.1	63.0	66.6	67.9	69.7	64.3	67.6	62.5	66.6	66.3	68.0	65.4	75.5
Eye diameter	45.4	49.7	47.7	47.4	45.7	44.1	48.1	50.2	46.6	47.3	45.5	47.4	47.2	49.0
Interorbital width			16.0	17.2					17.3			20.1		20.8
Maxillary length			51.7	46.4					48.5			49.6		48.7
3d dorsal ray length			52.3	63.6					60.3			60.7		62.5
3d anal ray length			53.2	58.3					53.3			57.8		58.5

ADDENDUM

After the manuscript for this paper had gone to press, a recent paper by Paulo de Miranda Ribeiro came to my attention (Alguns peixes pouco conhecidos ocorrendo na costa Brasileira, *Boletim do Museu Nacional, Rio de Janeiro, nova serie, zoologia*, no. 224, p. 1–11, 1961). In this paper, Miranda Ribeiro described and figured a specimen, apparently a priacanthid, which he designated as *P. altus*. The specimen was collected far offshore between Florianopolis and Laguna, Brazil (at latitude 28°45′ S., longitude 47°50′ W.), and is thus so far out of the geographical range given in the present paper for this species that it requires comment.

The specimen clearly is not *P. altus*. The reasons for this become evident when Miranda Ribeiro's description and figure are compared with my data and figures presented in this paper. Miranda Ribeiro did not include many pertinent facts which would positively identify his specimen, but it most closely resembles *Cookeolus boops* (Bloch and Schneider) and is from within the recorded range of that species. Although coming from within or near the ranges of the two western Atlantic species of the genus *Priacanthus*, it does not fit the descriptions of these two species. I have recently treated the four western Atlantic priacanthids with illustrations and a key (Caldwell, in press).

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SEXUAL MATURITY AND SPAWNING OF ALBACORE IN THE CENTRAL SOUTH PACIFIC OCEAN

By Tamio Otsu, *Fishery Research Biologist,* and Richard J. Hansen, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii

The albacore tuna, *Thunnus germo* (Lacépède), is found generally throughout temperate and tropical waters of the Pacific Ocean, where it is the basis of important fisheries for Americans and Japanese. The demand in America for canned albacore has steadily increased, and today this demand is met only by a considerable importation of frozen and canned fish. The Japanese, at present the principal suppliers of albacore, fish for this species along with other tunas in the tropical Indian and Atlantic Oceans as well as in the Pacific (Otsu, 1959).

As part of the research of the staff of the Bureau of Commercial Fisheries Biological Laboratory (Honolulu) a study was initiated in August 1957 of the gonadal development and spawning of albacore in the South Pacific Ocean. Such a study had previously been conducted on North Pacific albacore (Otsu and Uchida, 1959b). Presently it is not known whether the albacore fished by Americans and Japanese in the temperate North Pacific Ocean belong to the same population as those of the South Pacific. This study was undertaken to obtain (1) a broader understanding of the biology of the albacore and (2) a possible clue to the relation between fish occurring in the North and South Pacific Oceans.

Tag recoveries have shown that the albacore of the temperate North Pacific make oceanwide migrations and probably constitute a single intermingling population exploited by both Americans and Japanese (Ganssle and Clemens, 1953; Blunt, 1954; Otsu and Uchida, 1959a; Otsu, 1960). It is also known from previous studies that albacore do not spawn in temperate waters of the North Pacific (Otsu and Uchida, 1959b). There are indications that adult fish move south from temperate waters to spawn in subtropical waters, possibly to the west of, and in the general latitudes of, the Hawaiian Islands (Ueyanagi, 1957; Otsu and Uchida, 1959b). It is necessary to obtain similar information for albacore in the South Pacific before any study can be made of the total population structure of this important tuna resource.

The authors wish to acknowledge the excellent cooperation extended by the management and staff of the Van Camp Sea Food Co., in making this study possible. Donald Doran, former general manager, and his staff at the Van Camp Tuna Company cannery in American Samoa were instrumental in getting the gonad sampling accomplished. Mort Miles and Francis Yuhashi helped in many ways with the collecting, preserving, and shipping of samples. Poulima Tumanuvao and John Williams, Samoan cannery employees, faithfully sampled daily landings, made accurate length and weight measurements on the sampled fish, and kept excellent records which formed the basis of this study.

SOURCE OF MATERIALS

The tuna fishery based in American Samoa offers an excellent source of materials for the study of albacore spawning in the South Pacific Ocean. Albacore are landed throughout the year, making it possible to obtain samples continuously for the study of seasonal variation in gonad development. Furthermore, the great extent of the area fished makes possible the study of areal variations in spawning activity.

An account of the beginning of this tuna fishery is given by Van Campen (1954). At present (1960), the cannery in Pago Pago, American Samoa, is being served by a fleet of about 35 Japanese and 3 Korean longline fishing vessels. From its beginning in 1954, with a fleet of 7 boats and an albacore production of 270 tons, the fishery has continued to expand, until landings of albacore today exceed 12,000 short tons (fig. 1).

Note.—Approved for publication Aug. 7, 1961. Fishery Bulletin 201.

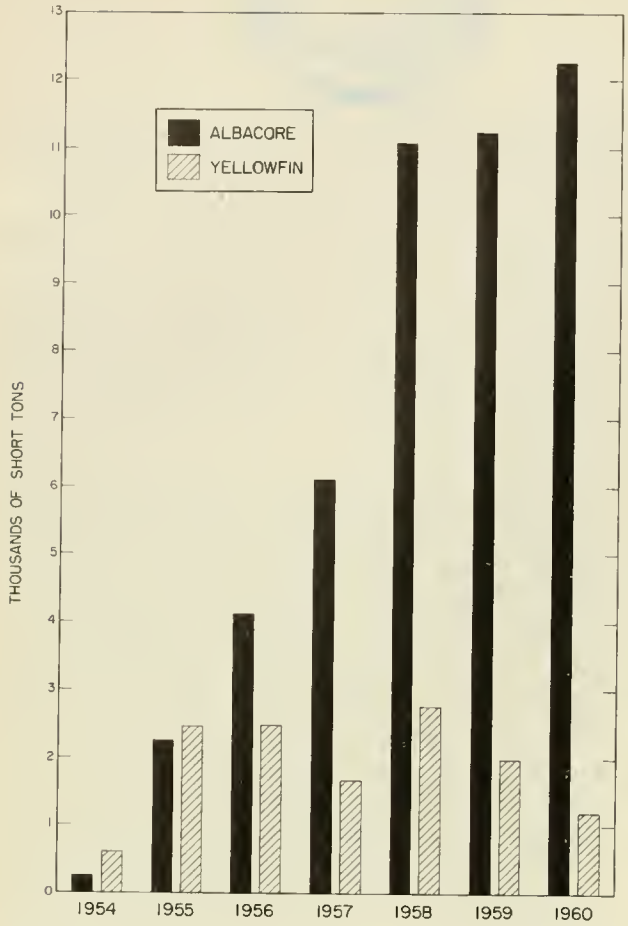

FIGURE 1.—Total annual albacore and yellowfin landings (tons) at the cannery in Samoa: 1954–60.

The fishing grounds, which in 1954 and early 1955 were chiefly in the vicinity of Samoa and to the north, have expanded to more distant and southerly waters. This shift in fishing grounds has been accompanied by a shift in species composition of the catch from predominantly yellowfin, *Neothunnus macropterus* (Temminck and Schlegel), to albacore (fig. 1). The boats range great distances in all directions from Samoa (fig. 2).

In August 1957, arrangements were concluded with the management and staff of the Van Camp Tuna Company to obtain gonad samples at the cannery from 7 randomly selected albacore from each landing. The fork length of each sampled fish was measured to the nearest millimeter, using a standard 1½-meter fish caliper, and the fish was weighed to the nearest ½ pound. The gonads were removed and placed in plastic bags, appropriately labeled, then kept frozen until received by our Honolulu laboratory. Additional information accompanying each gonad sample included the date of sampling, the fishing period (from which it was possible to tell the probable month of capture), and the locality of capture.

Although emphasis in this study was placed on the examination of ovaries, since previous studies had indicated that testes are generally unsatisfactory for the determination of developmental stages (June, 1953; Otsu and Uchida, 1959b), gonads of both sexes were collected in order to insure complete randomness in sampling.

The samples of gonads collected and shipped to Hawaii comprised 1,772 pairs; the approximate capture dates of the fish covered the period July 1957 to September 1958 (table 1). The sampled albacore ranged in size from 72 to 110 cm. (15 to 64 lbs.) (fig. 3).

TABLE 1.—*Gonads collected at the cannery in Samoa, July 1957 to September 1958*

Date	Number of landings sampled	Number of ovaries	Number of testes
1957			
July	2	7	7
August	19	51	75
September	17	42	74
October	9	24	37
November	7	22	27
December	16	62	50
1958			
January	26	60	118
February	20	55	77
March	21	65	81
April	21	74	73
May	15	47	58
June	26	89	91
July	28	101	95
August	27	76	120
September	2	7	7
Total	256	782	990

LABORATORY PROCEDURE

Upon arrival of the frozen samples from Samoa, they were thawed and preserved in 10-percent formalin. Laboratory examination of the formalin-preserved samples followed much the same procedure used and described in detail by Otsu and Uchida (1959b) in their study of North Pacific albacore spawning. Each pair of gonads was trimmed of extraneous tissue and weighed to the nearest 0.5 gram. No further work was done on testes. The ovaries were sectioned and examined under a microscope. The results of the previous study of ova sizes and characteristics of the albacore by Otsu and Uchida (1959b) indicated that

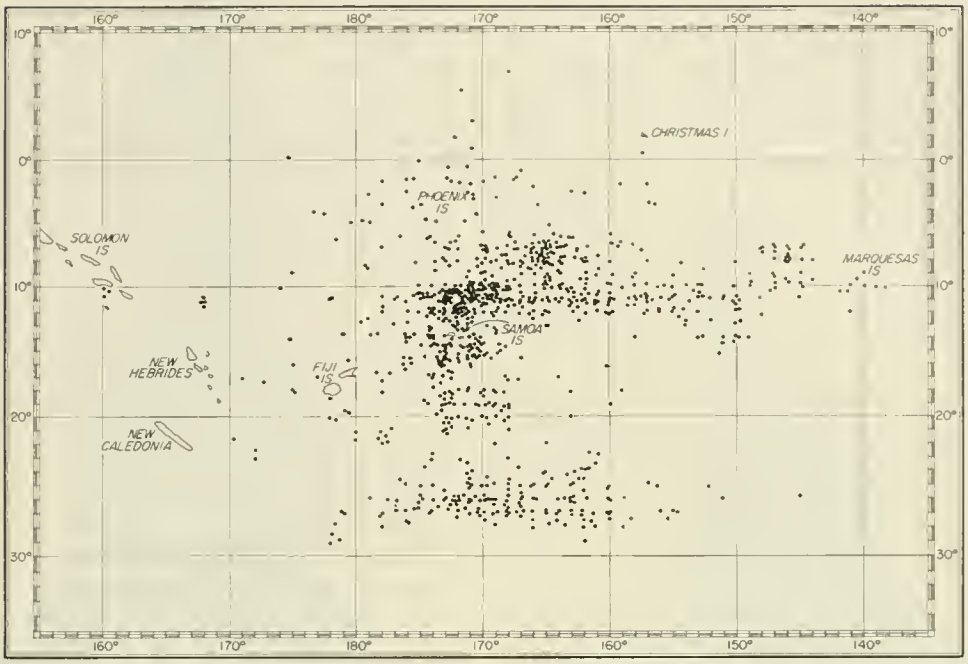

FIGURE 2.—Areas fished by the Samoa-based vessels. Each dot represents the approximate central position of one trip's fishing.

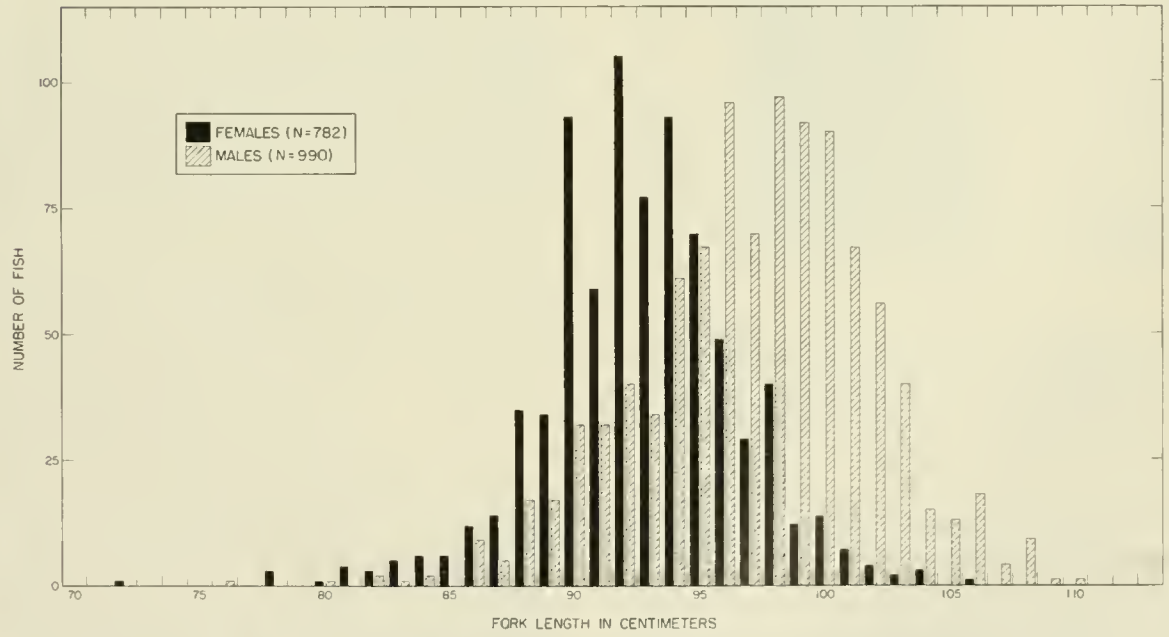

FIGURE 3.—Size of albacore sampled at the tuna cannery in Samoa, August 1957 to September 1958.

a gross examination of the ovaries would suffice. This consisted of recording the stage of development of the ovary by noting the general appearance and characteristics of the largest ova present. Additionally, 25 of the largest ova were measured to give an indication of the maximum sizes comprised in each ovary sample. For early developing ovaries, with ova in the primitive and early developing stages, no measurements were made; only the stage of development was noted.

DEVELOPMENTAL STAGES

Ovaries were classified as "early developing", "late developing", or "advanced", according to the stage of development of the largest ova present. The characteristics of ova in these stages have been described by Otsu and Uchida (1959b). Briefly they are:

Early developing.—In this stage the ovaries contain only the transparent primitive ova, or ova that are in the beginning stages of development and are semi-opaque from deposition of yolk granules.

Late developing.—This is a broad category in which the ova are completely opaque from the heavy accumulation of yolk granules; their diameters range from about 0.4 to 0.8 mm.

Advanced.—In this stage the ovaries are approaching ripeness. The largest ova are semitransparent and contain a conspicuous golden-yellow oil globule. These advanced ova, not fully ripe, range from about 0.7 to 1.0 mm. in diameter.

RESULTS

Seasonal variation in gonad development

Table 2 shows the number of ovaries of each developmental stage found each month. The six ovaries classified as advanced (2 each in Sept. and Oct. 1957 and Jan. 1958) contained ova in the transitional stage between late developing and advanced, just beginning to take on the characteristic semitransparent appearance. The ova diameters (0.60 to 0.64 mm.) resembled more closely the late developing than the advanced stages of Hawaiian albacore ovaries (Otsu and Uchida, 1959b). In comparison, the most highly developed albacore sampled in Hawaiian waters possessed ova with a modal diameter of 0.85 mm.

The percentage of ovaries in the late developing and advanced stages is shown for each month beginning with July 1957 (fig. 4). There is a gradual increase in development, with the peak appearing in December. In May, practically all of the ovaries are in the early developing stage. The increasing trend appears again after May. The 100-percent occurrence of the late developing

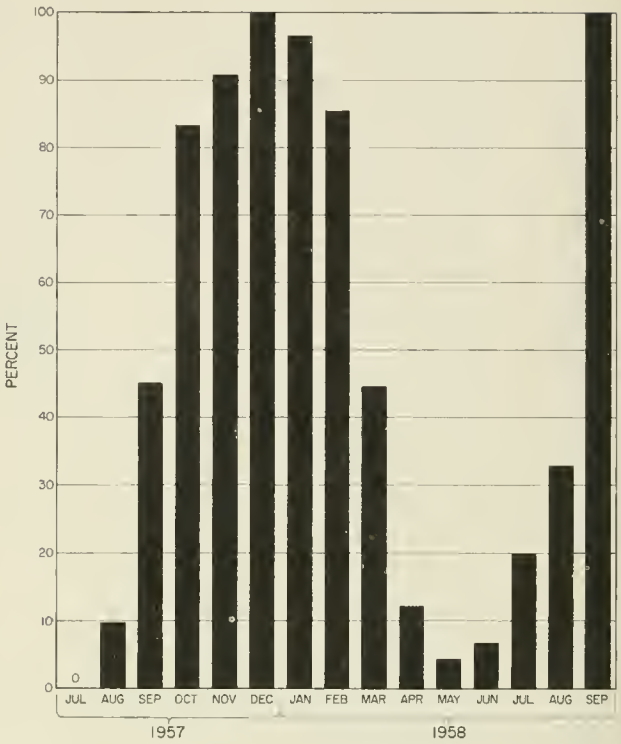

FIGURE 4.—Percentage of ovaries in the late developing and advanced stages, by month.

TABLE 2.—*Developmental stages of ovaries shown by month of capture*

Date	Number in each stage			Total
	Early developing	Late developing	Advanced	
1957				
July	7	0	0	7
August	46	5	0	51
September	23	17	2	42
October	4	18	2	24
November	2	20	0	22
December	0	62	0	62
1958				
January	2	56	2	60
February	8	47	0	55
March	36	29	0	65
April	65	9	0	74
May	45	2	0	47
June	83	6	0	89
July	81	20	0	101
August	51	25	0	76
September	0	7	0	7
Total				782

stage in September 1958 is probably due to the very small sample (7) collected during the month.

It seems clear from figure 4 that the peak of spawning activity in the central South Pacific occurs at some time during the southern summer months, between September and March. It seems logical to assume that the peak spawning period begins around December and extends into January or February, when the percentage of the late developing stage gradually decreases. This interpretation is based on the assumption that this decrease reflects a gradual development of the ovaries through the advanced, ripe, and spawning stages.

This southern summer spawning is in contrast to the albacore of the North Pacific, which appear to spawn during the northern summer months (Ueyanagi, 1957; Otsu and Uchida, 1959b).

Areal variation in gonad development

Since ovaries in the advanced stage were so few, and those in the ripe stage were entirely missing from the samples, we have considered late developing ovaries to be indicative of spawning fish. It has been postulated by Otsu and Uchida (1959b) that when albacore are close to spawning, they become unavailable to the hook and line fishery. There is also a distinct possibility that the ovaries develop very rapidly after passing the late developing stage (Ueyanagi, 1957) and that they are in the advanced stage for but a very brief interval before spawning takes place. This would then make sampling of the later stages a matter of slight chance and may well account for the small numbers of such stages found. Although the more advanced stages are missing from our collection, we believe that reasonable inferences as to spawning can be drawn from the occurrence of ovaries in the late developing stage.

In figures 5 and 6 and tables 3 and 4 are shown, by area and by time, the percentage of occurrence of late developing and advanced ovaries in the samples. Since the data revealed no clear longitudinal differences in the seasonal development of the ovaries (fig. 5), only the latitudinal differences are discussed here. The areas were arbitrarily divided latitudinally as follows: 0°–10° S., 10° S.–20° S., and 20° S.–30° S.

Some differences are apparent. In the area south of latitude 20° S. nearly all of the ovaries sampled were in the early developing stage, indicating that there is very little, if any, spawning in that area. On the other hand, in the area between 10° S. and 20° S., 287 out of 387 pairs of ovaries were found to be in the late developing stage, indicating that most of the albacore spawning south of the Equator takes place in these latitudes. Sampling was inadequate between the Equator and 10° S., but this area may probably be considered an extension of the middle area.

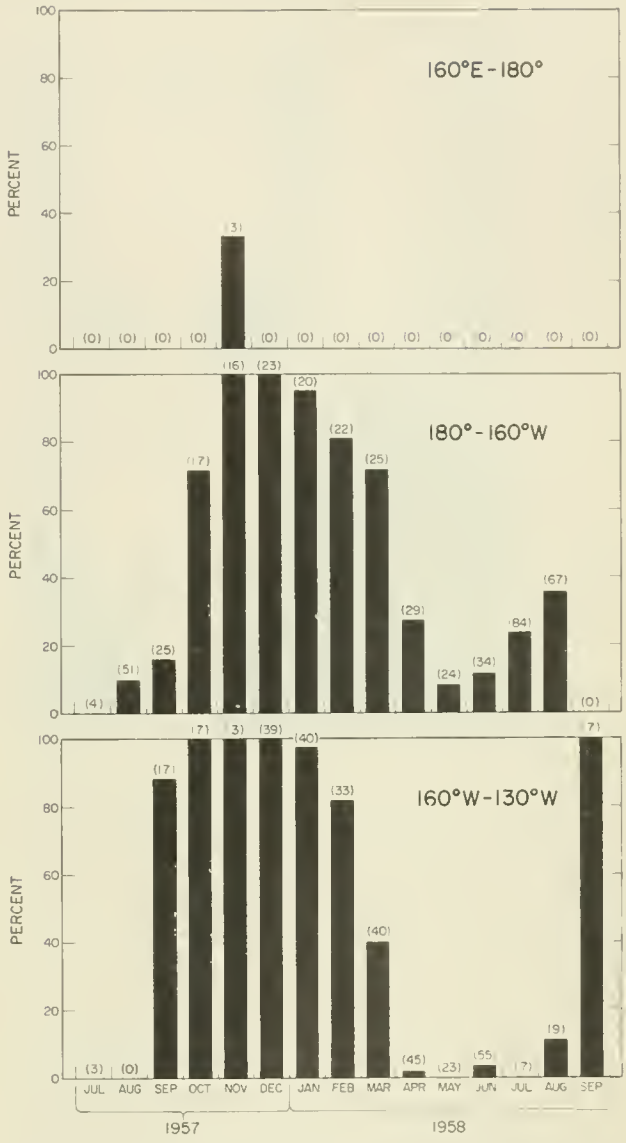

FIGURE 5.—Seasonal and longitudinal variation in ovary development, central South Pacific Ocean (0°–30° S.). (The percentage of late developing and advanced ovaries and the sample number are shown for each month.)

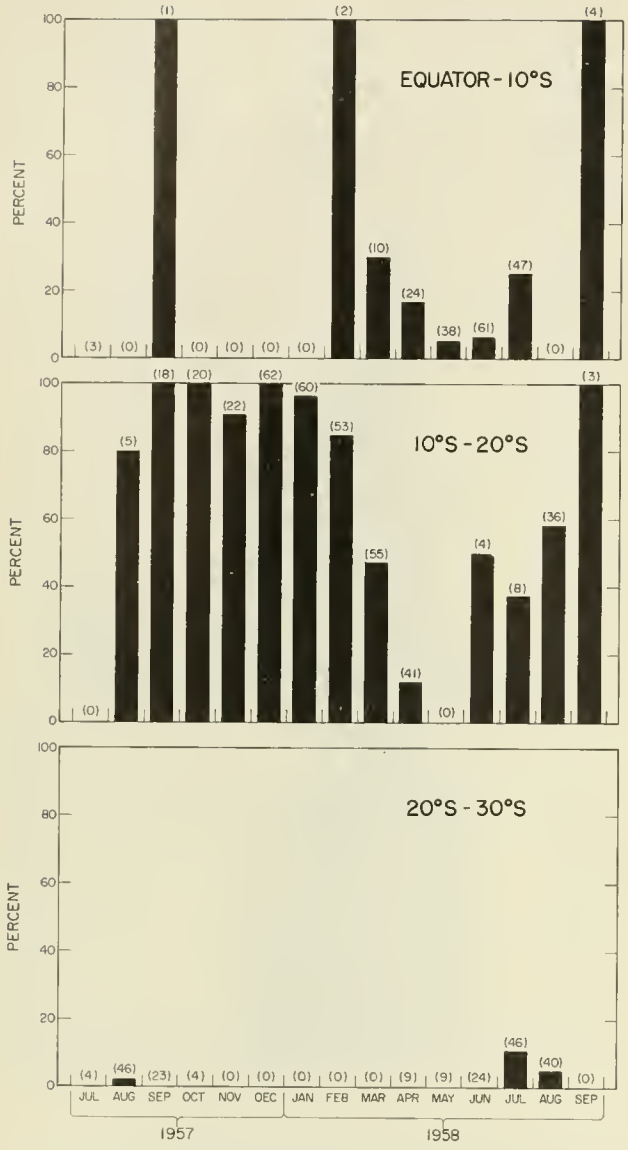

FIGURE 6.—Seasonal and latitudinal variation in ovary development, central South Pacific Ocean (130° W.–160° E.). (The percentage of late developing and advanced ovaries and the sample number are shown for each month.)

Unfortunately, the data are not as complete as desired. For example, no samples were obtained from the southernmost area during the period between November and March, which includes the apparent peak spawning season in the South Pacific. During these months the vessels seem to have confined their activities to the waters north of 20° S. latitude, either because inclement weather precluded their fishing farther south, or because fish were readily available in waters closer to their operating base. Catch records indicate that the latter has been the case, since landings continued high during this period.

TABLE 3.—*Seasonal and longitudinal variation in ovary development, central South Pacific Ocean (0°–30° S. latitude)*

Date	Longitude								
	160° E.–180°			180°–160° W.			160° W.–130° W.		
	Stage of development								
	Early	Late	Advanced	Early	Late	Advanced	Early	Late	Advanced
1957									
July	0	0	0	4	0	0	3	0	0
August	0	0	0	46	5	0	0	0	0
September	0	0	0	21	4	0	2	13	2
October	0	0	0	4	11	2	0	7	0
November	2	1	0	0	16	0	0	3	0
December	0	0	0	0	23	0	0	39	0
1958									
January	0	0	0	1	19	0	1	37	2
February	0	0	0	2	20	0	6	27	0
March	0	0	0	7	18	0	28	12	0
April	0	0	0	21	8	0	44	1	0
May	0	0	0	22	2	0	23	0	0
June	0	0	0	30	4	0	53	2	0
July	0	0	0	64	20	0	17	0	0
August	0	0	0	43	24	0	8	1	0
September	0	0	0	0	0	0	0	7	0
Total	2	1	0	265	174	2	185	149	4

TABLE 4.—*Seasonal and latitudinal variation in ovary development, central South Pacific Ocean (130° W.–160° E. longitude)*

Date	Latitude								
	0°–10° S.			10° S.–20° S.			20° S.–30° S.		
	Stage of development								
	Early	Late	Advanced	Early	Late	Advanced	Early	Late	Advanced
1957									
July	3	0	0	0	0	0	4	0	0
August	0	0	0	1	4	0	45	1	0
September	0	1	0	0	16	2	23	0	0
October	0	0	0	0	18	2	4	0	0
November	0	0	0	2	20	0	0	0	0
December	0	0	0	0	62	0	0	0	0
1958									
January	0	0	0	2	56	2	0	0	0
February	0	2	0	8	45	0	0	0	0
March	7	3	0	29	26	3	0	0	0
April	20	4	0	36	5	0	9	0	0
May	36	2	0	0	0	0	9	0	0
June	57	4	0	2	2	0	24	0	0
July	35	12	0	5	3	0	41	5	0
August	0	0	0	15	21	0	38	2	0
September	0	4	0	0	3	0	0	0	0
Total	158	32	0	100	281	6	197	8	0

The seasonal shift in fishing grounds, as indicated by the areas fished by Samoa-based vessels, may therefore reflect movements of the fish related to their spawning in the more northern waters during the southern summer months.

Minimum size of spawning fish

It was first reported by Ueyanagi (1955) and later supported by the findings of Otsu and Uchida (1959b) that female albacore attain sexual maturity and thus may first spawn at about 90 cm. in length. Because of the larger sample now available a further examination was made of this point.

Figure 7 shows the developmental stage of each ovary plotted by fish length and by ovary weight. The data show that some fish are already mature at 86 cm. This is not far different from previous results. The smallest fish found to be mature in the central equatorial Pacific measured 89.1 cm. (Otsu and Uchida, 1959b), and the smallest from the western Pacific (Ueyanagi, 1957) was 87 cm. long. Some albacore may therefore become sexually mature and spawn for the first time at a size of about 86 cm.

As for the males, Ueyanagi (1957) judged from their general appearance and oozing of milt that testes weighing more than 150 grams were probably ripe. By plotting testis weight against fish length, he showed that the smallest fish having testes weighing more than 150 grams measured 97 cm., and he postulated that length to be the minimum size of sexual maturity in males as

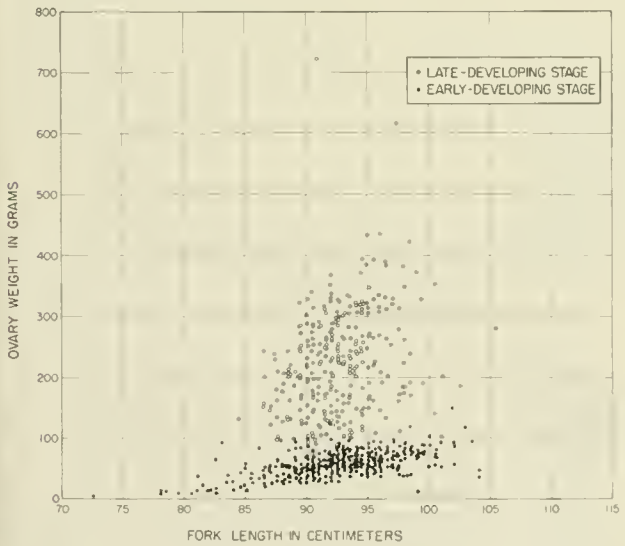

FIGURE 7.—Ovary weight plotted by fish size.

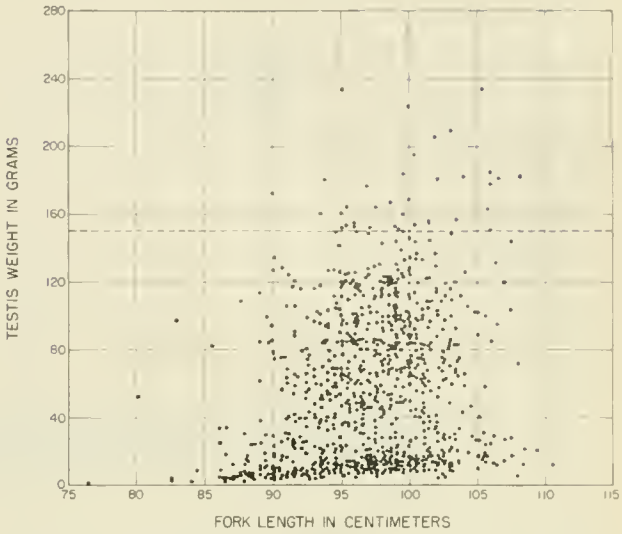

FIGURE 8.—Testis weight plotted by fish size. Dashed line is at 150 grams, the weight used by Ueyanagi (1957) as a criterion of ripeness.

contrasted with 87 cm. for females. Following Ueyanagi's lead, we have plotted testis weight against fish length (fig. 8). It can be surmised from this figure that some male albacore are probably sexually mature when they attain a length of about 90 cm., since testes weighing more than 150 grams already appear at this size. However, lacking more objective means of determining maturity of the males, it cannot be said with certainty that this is the size at which male albacore are first capable of spawning.

Size of the albacore

As shown in figure 3, the sampled fish ranged between 72 and 110 cm. (15 and 64 lbs.). It is interesting to compare the sizes of these fish with those taken in Hawaiian waters, which are believed to be part of the reproductive segment of the North Pacific population. Although very few albacore are landed in the Hawaiian fishery, they are generally very large (see fig. 9, which is based on fig. 7 in Otsu and Uchida, 1959b). Albacore landed in Hawaii in 1955 and 1956 ranged in size between 93 and 128 cm. (33 and 93 lbs.), but females appeared to reach their maximum size at 112 cm. In the South Pacific samples, the largest female measured 106 cm. (fig. 3).

Perhaps most significant is that while the female fish in the two areas were thus of comparable sizes, there was a virtual absence of males larger

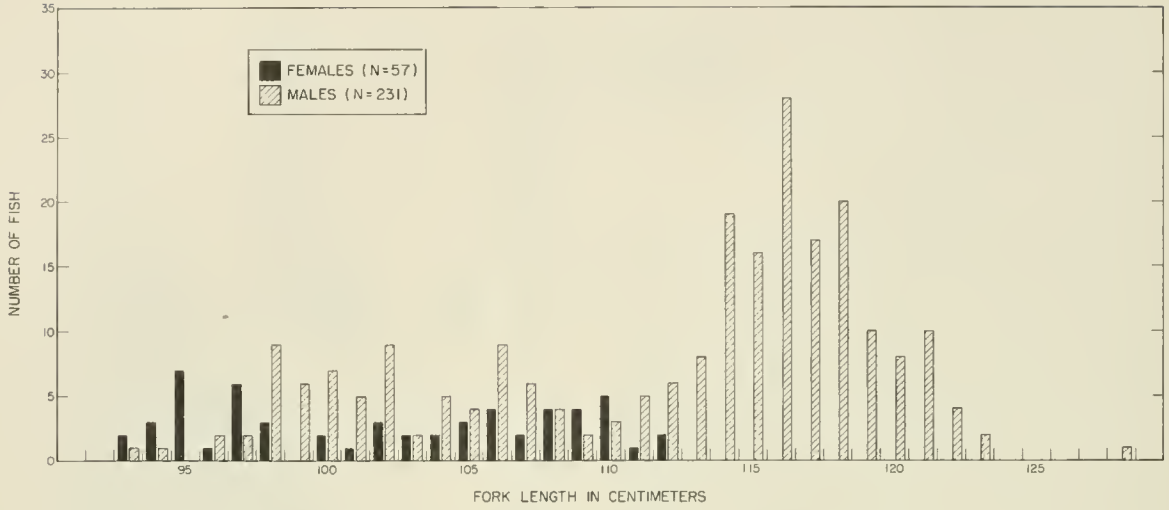

FIGURE 9.—Size of albacore taken in the Hawaiian longline fishery, 1955–56.

than 110 cm. in the South Pacific. A similar lack of large males was found in samples from the central equatorial Pacific (Otsu and Uchida, 1959b); the significance of this difference in size composition between Hawaiian waters and more southern areas is not known. Further study is needed concerning the distribution of these large males.

The most highly developed ovaries reported to date have come from waters around the Hawaiian Islands in the North Pacific (Otsu and Uchida, 1959b) and from the area of the Sunda Islands in the Indian Ocean (Ueyanagi, 1955). None as advanced in development has yet been collected from the central equatorial Pacific or the South Pacific Ocean. The fish taken in the Indian Ocean are also large, falling intermediate between the Hawaiian and the central South Pacific albacore. Despite the apparent absence of the group of largest males in the central South Pacific, it appears certain that the males available to the longline fishery there are generally all adults which are already capable of spawning.

DISCUSSION

Our data suggest that albacore in the central South Pacific Ocean spawn during the southern summer months. This finding is based on the percentage occurrence of ovaries in the late developing stage for each month in which samples were obtained. Since only six pairs of ovaries were found in which development of the ova was beyond the late developing stage, the occurrence of ovaries in the late developing stage was used as an index of spawning fish. The inherent weakness in our assumption, particularly in assessing exact spawning grounds and spawning seasons, is that the time of spawning cannot be determined precisely from the occurrence of fish in this stage of ovary development, in the absence of any knowledge of the rate of ova development. The gradual increase in the proportion of late developing ovaries in the monthly samples from the low point in May to a peak in December, with a gradual decrease thereafter, suggests that spawning must take place during the southern summer months. Depending upon the rate of ova development, albacore may be spawning during only a portion of that period, and that portion may be towards the end, when the percentage of developing ovaries is decreasing.

The weakness in the data is also evident in attempting to determine the spawning grounds. Our data suggest that the bulk of the spawning activity is confined to the north of 20° S. latitude. The data also indicate no east-west differences in spawning activity within the extent of our sampling (fig. 5). In the absence of ovaries of more advanced development, these results may be questionable. There may be sufficient time between the late developing and ripe stages to permit considerable migration. No purposeful spawning migration can be detected from the data at hand. Until more definite findings are made by the cap-

ture of fish near spawning condition or by the collection and identification of fertilized ova or larvae, we can only conjecture that albacore in the South Pacific spawn over an extended area north of 20° S. latitude. The data indicated no apparent differences in size between albacore found in the area north of 20° S. latitude and those found south of 20° S. latitude (fig. 10). Fish smaller than 86 cm., and presumably sexually immature, were sampled in both areas, although they were very few. It appears that adult fish are distributed over the entire range of our sampling, but that their seasonal movements are such that spawning occurs largely in the more northern area.

Perhaps most significant in our findings is that the albacore in the South Pacific Ocean spawn during the southern summer months, in contrast to the northern summer-spawning of the North Pacific albacore (Ueyanagi, 1957; Otsu and Uchida, 1959b). This difference in spawning seasons constitutes some evidence that the South Pacific and North Pacific albacore stocks are independent of each other. Tag recoveries have indicated that the three albacore fisheries in the temperate North Pacific Ocean, conducted by the Japanese off their coastal waters in spring, by Americans off the Pacific coast of the United States in summer, and by the Japanese in midocean during the winter months, are exploiting a single population (Otsu, 1960). There is some evidence that fish occurring within the North Equatorial Current are the reproductive segment of the same North Pacific population (Ueyanagi, 1957). What is not known at present is the relation of these fish to those occurring in the Southern Hemisphere, and presently being fished by Japanese and South Korean longliners in midocean and by Chilean fishermen in their coastal fishery. Pending more definitive results from further tagging, our data suggest that an independent population exists on each side of the Equator, and that

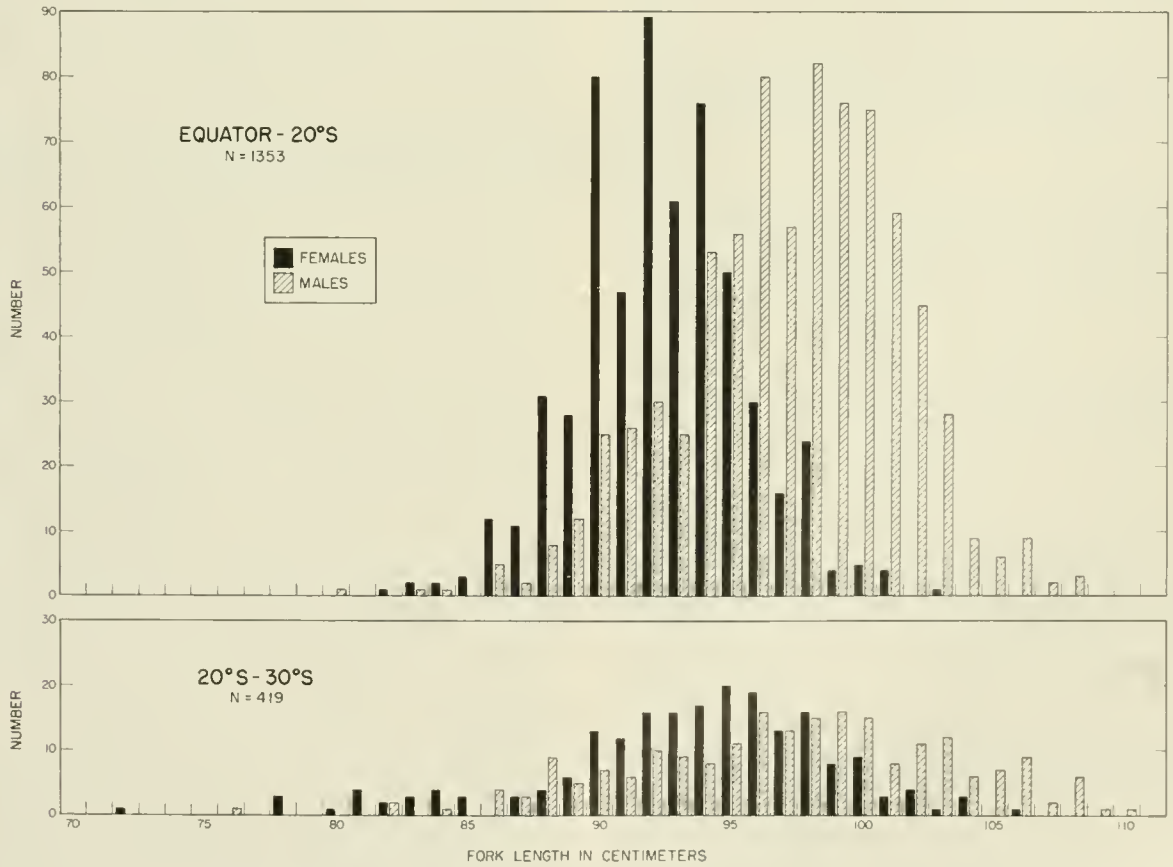

FIGURE 10.—A comparison of the sizes of albacore taken between the Equator and 20° S. and those between 20° S. and 30° S. latitude (by sex).

each is distributed in an approximate mirror image of the other. In the North Pacific, only the albacore in temperate waters are being exploited commercially. Albacore are taken incidentally to other species and in small numbers in subtropical and tropical waters, i.e., between 25° N. and the Equator.

Spawning is believed to occur in subtropical waters, roughly between 10° N. and 25° N. latitude in the western Pacific during the northern summer months. The situation is somewhat different in the South Pacific. The major exploitation in the South Pacific at present is of the subtropical resource of albacore in the area between 10° and 30° S. latitude. Furthermore, the only fishery equivalent to the North Pacific temperate water fisheries is the relatively small coastal fishery of Chile. However, data published by Japan's Nankai Regional Fisheries Research Laboratory (1959), reproduced here as figure 11, indicate the presence of smaller albacore south of the present central South Pacific fishing grounds (south of 30° S. lat.). These albacore appear to be the counterpart of the northern temperate-zone albacore. While there is no extensive fishery for albacore in these southern temperate waters today, there is a likelihood that a large resource is present (Suda, 1956).

While not exactly alike, the distributions follow a similar pattern on both sides of the Equator, with the smaller nonspawning fish occurring in the higher latitudes, and the larger spawning fish in the lower latitudes. Because of the general scarcity of albacore in equatorial waters, there appears little likelihood of any great interchange of fish between the two groups.

SUMMARY

This study is based on the examination of 1,772 pairs of albacore gonads collected at the tuna cannery in American Samoa between August 1957 and September 1958. The 782 female and 990 male gonads were collected randomly from 256 landings made by Japanese longline vessels.

Upon receipt of the frozen gonads from Samoa, they were thawed and preserved in 10-percent formalin. Each pair was weighed, and ovary sections were examined microscopically. The stage of development was determined on the basis of the general appearance and characteristics of the largest ova present. No detailed examination was made of the testes.

Only six ovaries were found to be in the advanced stage of development; these contained ova which were just beginning to take on the semitransparent appearance characteristic of this stage. The remainder of the ovaries were in all degrees of development preceding this stage.

From the monthly occurrence of the more mature stages (late developing and advanced), it was found that the peak of spawning activity in the central South Pacific is during the southern summer months at some time between September and March. This is in contrast to the albacore of the North Pacific, which appear to spawn during the northern summer months.

The examination of the data for areal variations in ovary development revealed no clear longitudinal differences. Latitudinally, nearly all of the more highly developed ovaries were obtained from fish captured north of 20° S., with the bulk between 10° S. and 20° S. latitude. The data indicated that there is little, if any, spawning in areas south of 20° S. latitude.

Plotting the developmental stage of each ovary against fish size revealed that female albacore become sexually mature and spawn for the first time at a size of about 86 cm. This is a slightly lower estimate of the minimum size of first spawning than previously reported (90 cm.).

The sampled fish ranged between 72 and 110 cm. (15 and 64 lbs.). In comparison, the Hawaiian albacore which are believed to be a part of the reproductive segment in the North Pacific are larger, ranging between 93 and 128 cm. (33 and 93 lbs.). A closer examination of the data shows that females are of comparable sizes in both areas, but that the very large males are missing from the South Pacific samples. It appears certain, however, that the males available to the longline fishery in the central South Pacific are nearly all adults which are already capable of spawning. The significance of this size difference in the males between the two areas is not clear.

Although the data are such that the precise spawning area or season could not be determined, the fact that the peak of spawning in the South Pacific occurs during the southern summer months, as contrasted with the northern summer spawn-

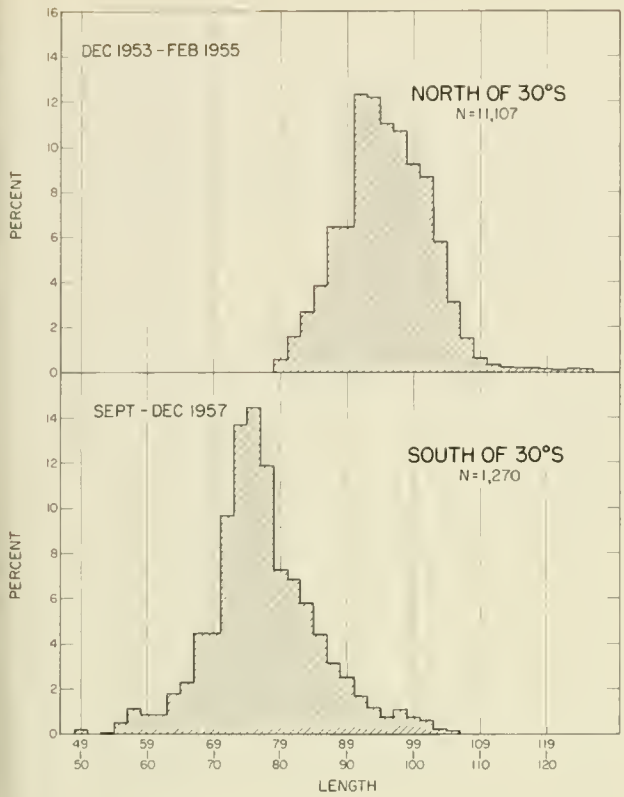

FIGURE 11.—Length frequencies of albacore in the South Pacific Ocean. (Japanese data reproduced from the report for 1959, figure 7, page 319, of the Nankai Regional Fisheries Research Laboratory.)

ing of the North Pacific albacore, constitutes evidence that the stocks in the South Pacific and the North Pacific are independent of each other.

The major exploitation in the South Pacific at present is of the subtropical resource of albacore in the area between 10° S. and 30° S. latitude. Japanese data indicate the presence of smaller albacore south of the present fishing grounds (south of 30° S.). These smaller fish may be part of a large resource not presently exploited, the counterpart of the North Pacific temperate water albacore.

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HYDROLOGICAL CHARACTERISTICS OF TAMPA BAY TRIBUTARIES

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This investigation is part of a study of Tampa Bay and adjacent neritic waters in connection with an effort to control the Florida red-tide menace. The Florida red tide is a natural fish-killing phenomenon in the waters along southwest Florida coast and is always associated with discolored water containing dense populations of *Gymnodinium breve*, a naked dinoflagellate. The primary objective was the collection of sufficient data to observe the natural levels and seasonal fluctuations of salinity, total phosphorus, inorganic phosphate, nitrate-nitrite nitrogen, and total dissolved copper in the Hillsborough, Alafia, Little Manatee, and Manatee Rivers which flow into Tampa Bay. Copper was included in this hydrological survey because of its high toxicity to laboratory cultures of *Gymnodinium breve*. Thus, copper was of particular interest as a possible limiting factor in the growth of *G. breve* in its natural surroundings. A secondary objective was to observe the influences of precipitation and the geological formations underlying the area upon the chemical composition of these rivers.

The chemical composition of the rivers has an important bearing on general problems of coastal oceanography (Ketchum, Redfield, and Ayers, 1951). Furthermore, it is essential that the chemical composition of the river waters be known for proper evaluation of the relative importance of the Tampa Bay area to red-tide research and other estuarine studies (Rochford, 1951; Spencer, 1956; and Manaché, 1958). Although the chemical composition of some Florida rivers has been studied previously by the U.S. Fish and Wildlife Service (Graham, Amison, and Marvin, 1954; Finucane and Dragovich, 1959; Dragovich and others, 1961); Geological Survey, Branch of Surface Waters, University of Florida (Specht, 1950); and by the Florida Geological Survey (Odum, 1953), little hydrological information has been gathered for the rivers flowing into Tampa Bay.

The authors are indebted to William B. Wilson for numerous valuable suggestions during this study. John A. Kelly, Jr., and John H. Finucane provided technical assistance.

MATERIALS AND METHODS

From October 1, 1958, through December 31, 1959, monthly collections of surface and bottom waters were made at eight stations (fig. 1). Samples for all analyses were taken with a weighted polyethylene container. Samples for total phosphate-phosphorus, inorganic phosphate-phosphorus, and nitrate-nitrite nitrogen were immediately transferred from the containers into 200-mm. culture vials which were capped with polyethylene-lined screw caps and quickly frozen. Samples for the determination of copper and salinity were transferred into 250-ml. glass-stoppered bottles, and those for salinity into 4-oz. prescription bottles. All containers used for sampling were chemically cleaned prior to use.

The following methods of analysis were employed:

Water temperature: Céntigrade thermometer graduated in tenths of a degree.

Salinity: Mohr-Knudsen method (Knudsen, 1901).

Total phosphate-phosphorus: Harvey (1948) method.

Inorganic phosphate-phosphorus: Robinson and Thompson (1948) method.

Nitrate-nitrite nitrogen: Zwicker and Robinson (1944) method as modified by Marvin (1955).

Copper: Hoste, Eeckhout, and Gillis (1953) method.

Samples taken for copper analyses were filtered. Samples collected for phosphorus and nitrogen determinations were not filtered.

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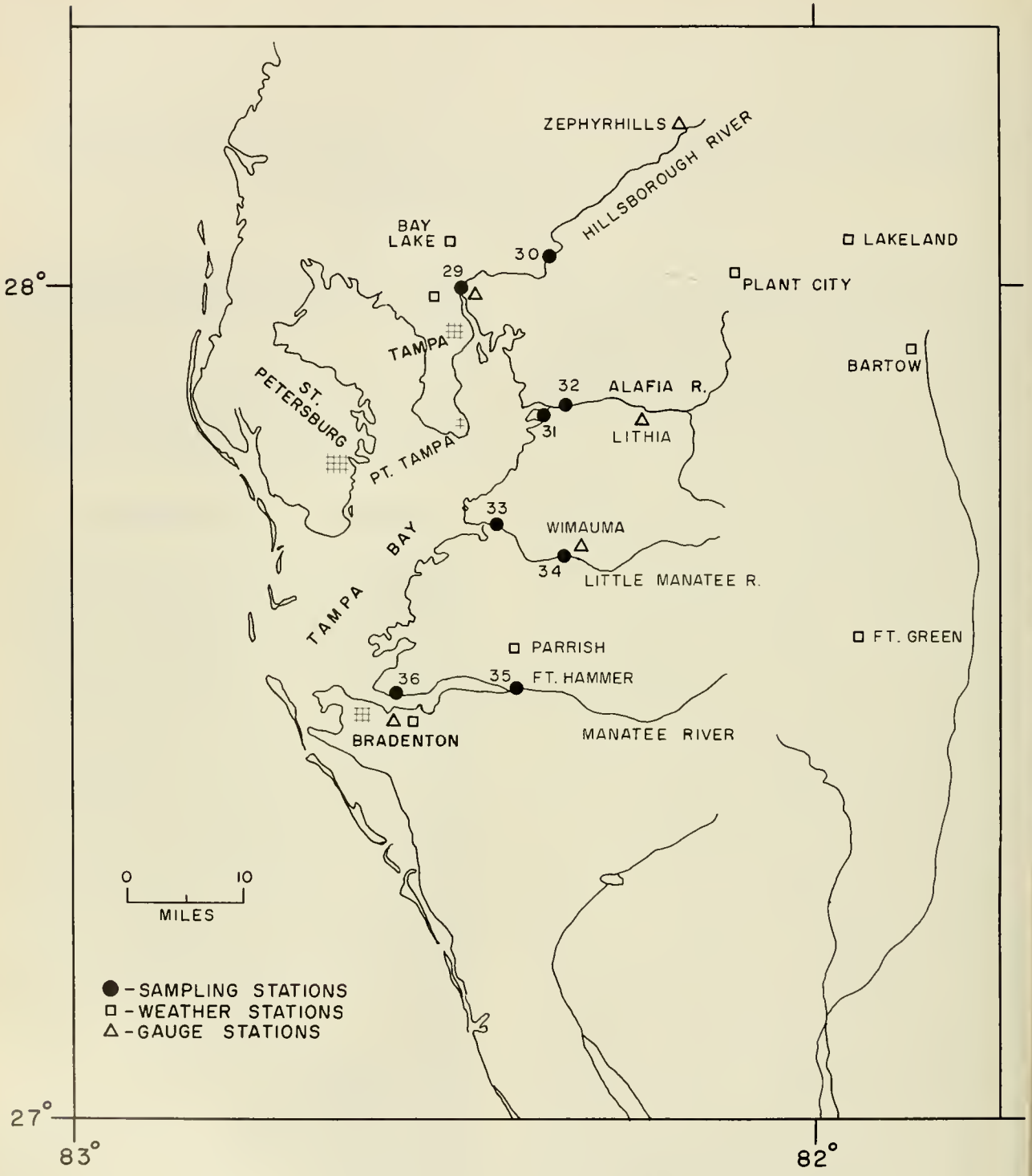

FIGURE 1.—Tampa Bay area showing rivers and sampling stations.

GENERAL DESCRIPTION OF THE AREA

The Hillsborough, Alafia, Little Manatee, and Manatee Rivers are relatively small and short, with sources less than 70 miles inland (fig. 1). These rivers are the main arteries of the Tampa Bay drainage basin, and all four river mouths are subject to tidal action. The mean range of tide is 1.9 feet at the lower end of Tampa Bay, 2 feet at Port Tampa, and 2.2 feet at Tampa. The extreme ranges at Port Tampa and at Tampa are 2.5 and 2.9 feet, respectively. Strong northerly winds lower the water level about 2 feet while strong southwesterly winds raise the water level about 1.5 feet.

Five gaging stations (fig. 1) are maintained in the rivers by the U.S. Geological Survey, Branch of Surface Waters, for the purpose of obtaining river discharge data.

Outstanding geological characteristics of the area are large phosphorus and limestone deposits. The major deposits containing phosphate are the Hawthorn (Miocene), Alachua (Pliocene), and Bone Valley (Pliocene) formations (fig. 2). Although the soils are high in lime and phosphorus, they are poor in copper, zinc, and manganese (Fuestel and Byers, 1933). The copper level has been supplemented in recent years in the citrus and truck farming areas by the addition of fertilizers of high copper content. Patches of peat and muck soils are scattered throughout the Tampa Bay drainage basin, although not to the extent observed in the Everglades. The detailed geology of the investigation area has been discussed by Cooke (1945).

The rainy season in the Tampa Bay area usually extends from June to October, and the streams reach seasonal high stages during late summer and early fall. The mean annual precipitation compiled from five centers (Bartow, Bradenton, Lakeland, Plant City, and Tampa) for the past 29 years (1931–59) is 53.5 inches.

The prevailing winds are easterly. The maximum wind velocity in the past 57 years was 75 miles per hour, while the mean velocity was 8.4 miles per hour. The Tampa Bay area has subtropical temperatures, generally with maxima in August and minima in January.

RESULTS

The water temperature ranged from 15.0° to 30.5° C. during this investigation. The seasonal decline in temperature in all rivers began in November during both observation years, reaching the seasonal minimum in December, which was followed by a sharp rise in January (figs. 3, 4, 5, and 6). From January through March, the temperature increased slightly in the Little Manatee River. In the Hillsborough, Manatee, and Alafia Rivers, a slight increase was recorded from January through February, followed by a drop in March. From March to May, temperature increased sharply in all rivers and remained variably high from May to October.

The frequency distribution of the temperature differences between surface and bottom ranged from 0.0° C. to 0.5° C. in 83.3 percent of the samples; 0.6° C. to 1.0° C. in 10.9 percent of the samples; and 1.1° C. to 3.1° C. in 5.8 percent of the samples. This distribution indicates close similarity between the surface and bottom temperatures.

The maximum salinity, 24.83 °/₀₀, was observed at the bottom of station 36 while a minimum of 0.04 °/₀₀ was recorded at stations 34, 35, 30, 31, and 32 (figs. 3, 4, 5, and 6). The salinity values indicated that station 30, Hillsborough River, and station 34, Little Manatee River, possessed limnetic characteristics throughout the observation period. Their respective ranges were 0.04 °/₀₀ to 0.32 °/₀₀ and 0.04 °/₀₀ to 0.48 °/₀₀. At all remaining stations much greater variation in salinity was noted.

Total annual precipitation in the Tampa Bay area was 57.4 inches in 1958 and 82.1 inches in 1959. The precipitation regime for the Hillsborough and Alafia drainage areas differed from that of the Little Manatee and Manatee River areas, the latter having more rain during the summer months (figs. 3, 4, 5, and 6). The early onset of the rainy season in March was most pronounced in the Hillsborough and Alafia areas.

In the Hillsborough and Alafia River drainage areas, maximal discharges began in March and, with the exception of a decline in May, remained variably high through October for the Hillsborough, and through September for the Alafia

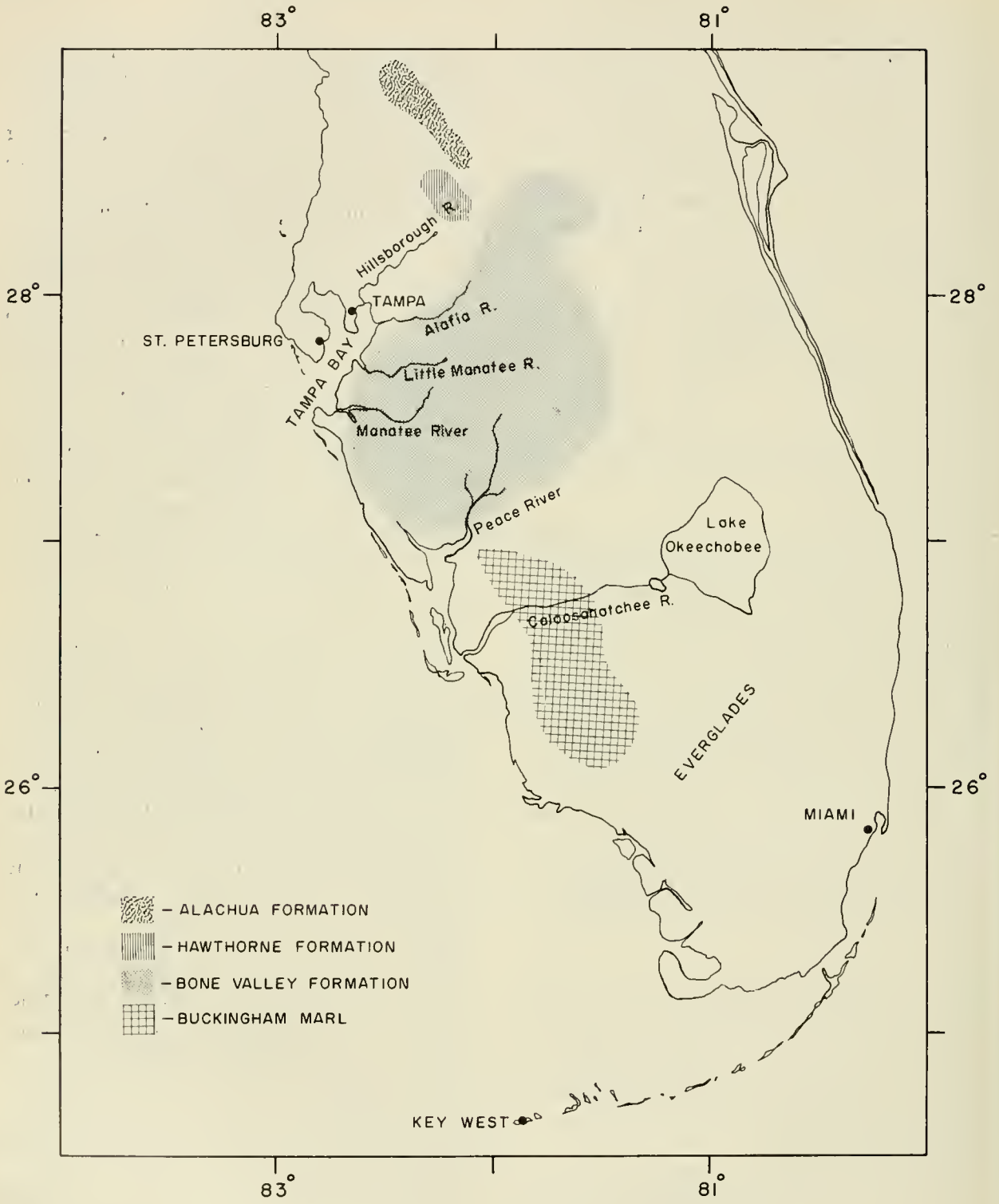

FIGURE 2.—Map of surface phosphate-bearing formations (after Cooke, 1945).

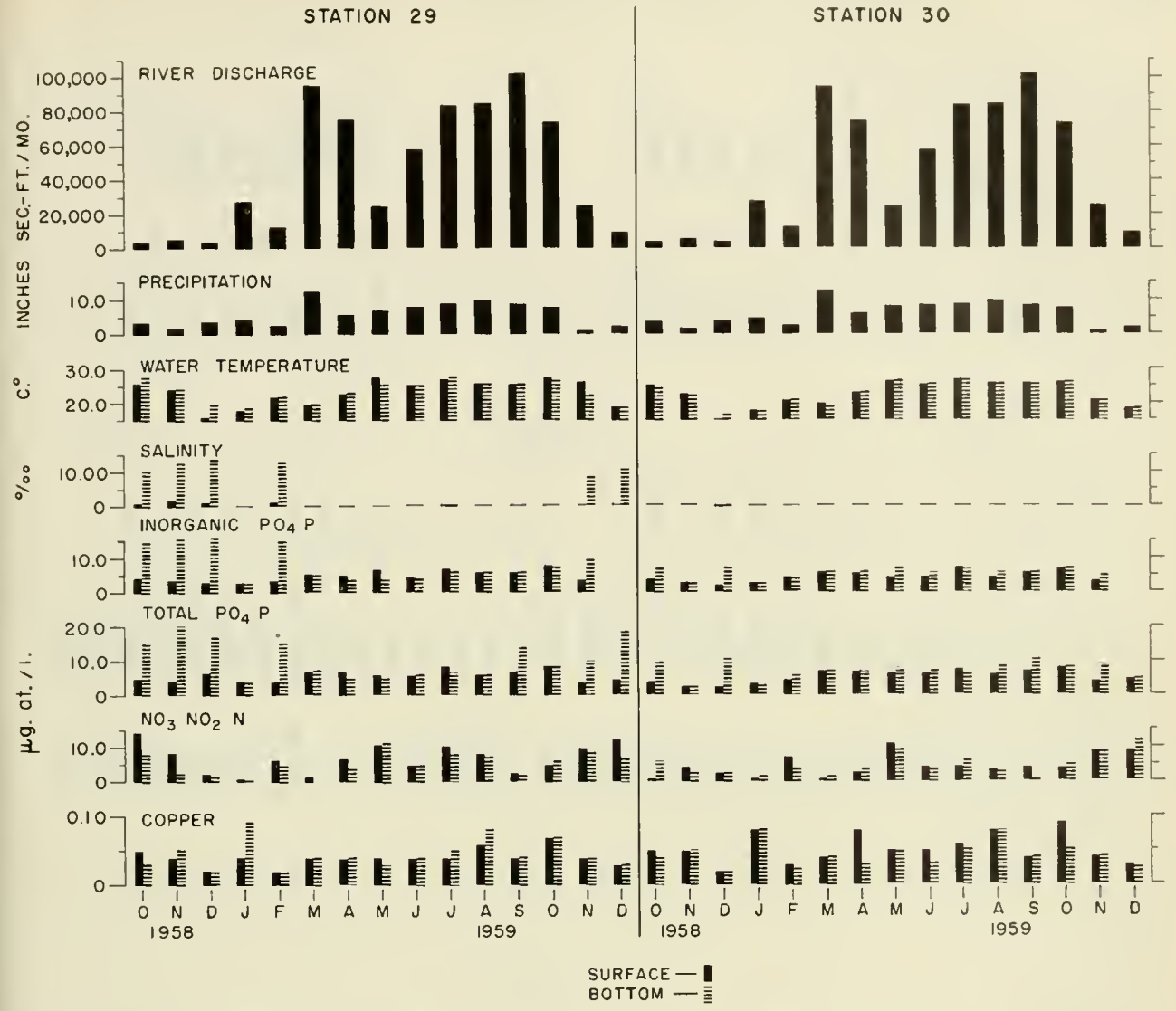

FIGURE 3.—River discharge, precipitation, and hydrological properties of Hillsborough River, Florida, October 1958–December 1959.

River. In the Little Manatee River the maximum discharges were from March through September. Data for October, November, and December 1959 are available only for the Hillsborough River. The river discharges were considerably higher in the Hillsborough and Alafia Rivers than in the Little Manatee and Manatee Rivers (figs. 3, 4, 5, and 6). The maximum discharge for the four rivers for the water year, beginning October 1958 and ending September 1959, was observed in the Hillsborough River (564,244 second-feet per day). The minimum discharge was recorded in the Manatee River (82,899 second-feet per day).

The concentrations of total phosphorus for all rivers varied from 2.5 µg.at./l., observed at the Hillsborough River at station 30, to 60.5 µg.at./l. recorded in the Alafia River at station 32.

The concentrations of total phosphorus in the Alafia River are extremely high in comparison to those in the other three rivers. The average total phosphorus value of 39.2 µg.at./l. for the Alafia River is 3.1 times that of the average value (12.6 µg.at./l.) observed in the next highest river, the Little Manatee. The monthly variations in phosphorus were similar at stations 31 and 32 which are 2.5 miles apart.

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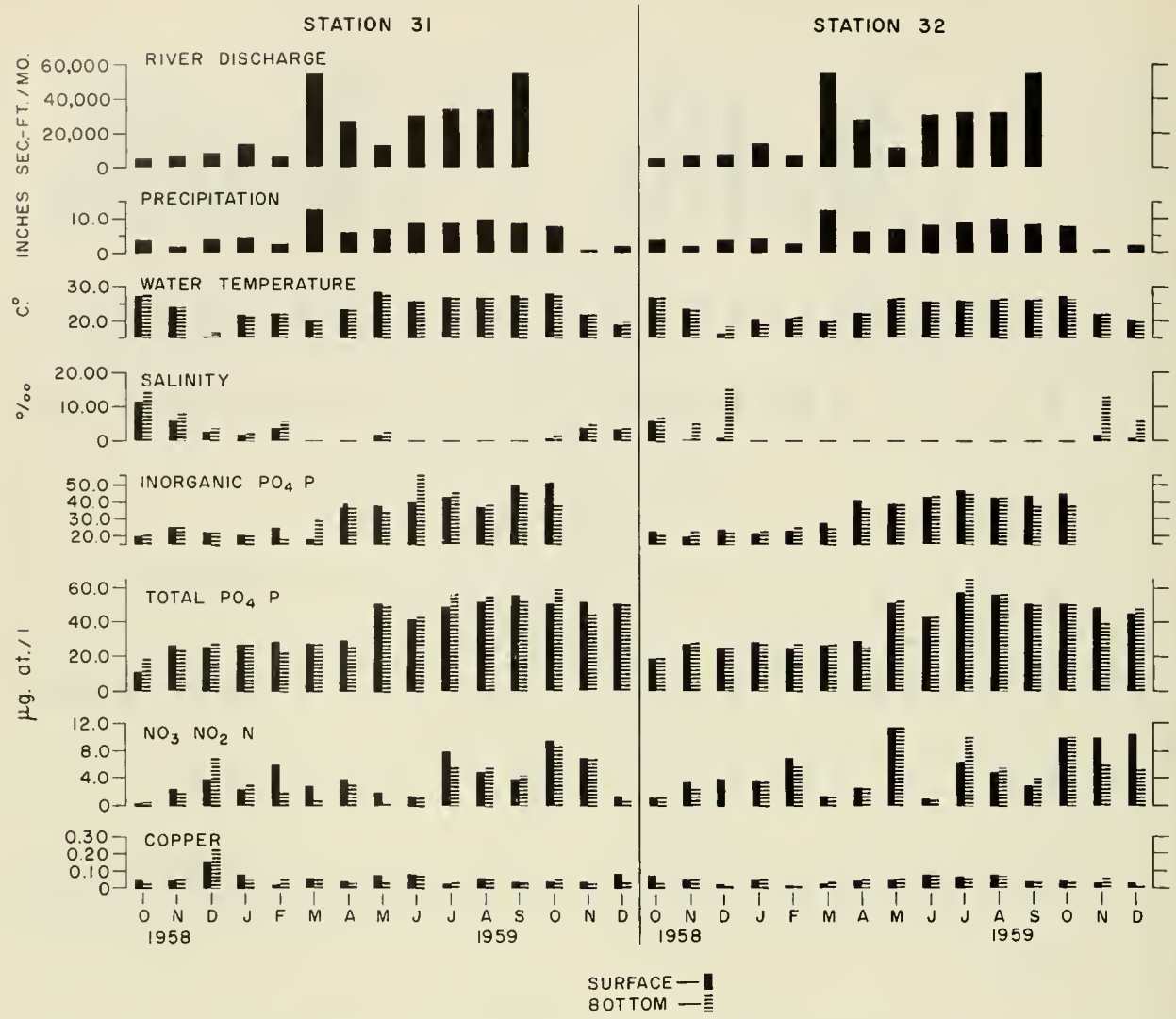

FIGURE 4.—River discharge, precipitation, and hydrological properties of Alafia River, Florida, October 1958–December 1959.

Concentrations of total phosphorus in the Little Manatee River were in turn higher than in the Manatee River, which showed higher concentrations downstream, with little difference between surface and bottom values (fig. 5).

The lowest concentrations of total phosphorus were observed in the Hillsborough River. In this river the vertical distribution of total phosphorus for the entire period showed higher values near the bottom whenever bottom salinity values were above normal (table 1). In March an increase in surface concentrations of total phosphorus and vertical homogeneity was evident. The surface and bottom total phosphorus concentrations remained variably high until the reappearance of stratified conditions in November. The distribution of total phosphorus at upstream station 30 was somewhat similar to that of station 29, but with greater vertical homogeneity (fig. 3).

The spatial and temporal distribution pattern of inorganic phosphate-phosphorus in the rivers was essentially the same as that of total phosphate-phosphorus (figs. 3, 4, 5, and 6). The mean inorganic phosphate values for the individual rivers represented 77 to 95 percent of the total. Organic phosphorus exceeded inorganic on only one occasion, at station 29 during September at the period of maximum discharges. Unusually high

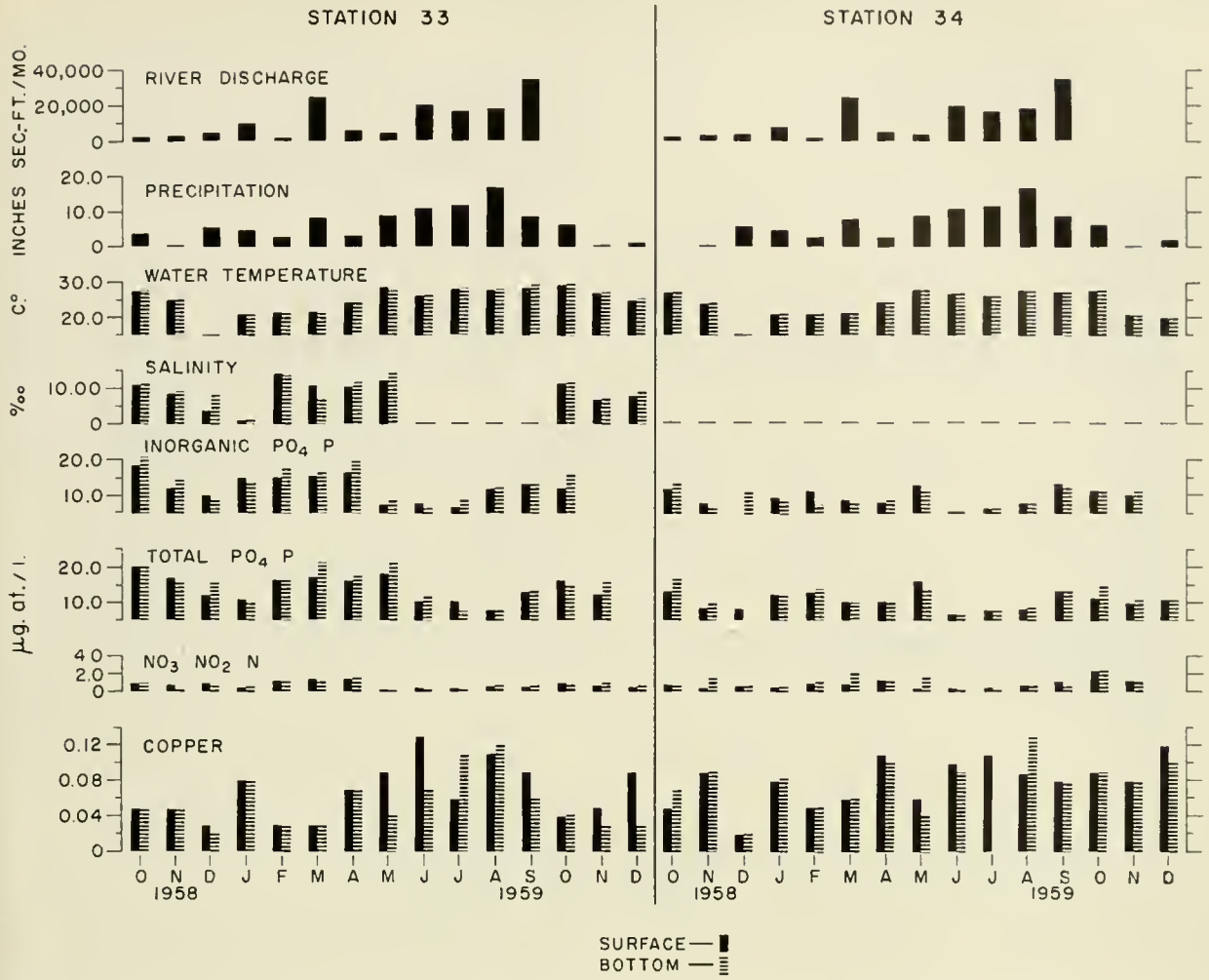

FIGURE 5.—River discharge, precipitation, and hydrological properties of Little Manatee River, Florida, October 1958–December 1959.

concentrations of organic phosphorus were observed in the Alafia River. High concentrations of inorganic phosphate-phosphorus in May were accompanied by high values of organic phosphorus (10.2–16.8 μg.at./l.). From May through October, with the exception of two values (0.0 and 0.2 μg.at./l.), the concentrations of organic phosphorus remained high.

Concentrations of nitrate-nitrite nitrogen in all rivers varied from 0.1 to 13.7 μg.at./l. Values for the Hillsborough and Alafia were 2 to 10 times higher than those for the Little Manatee and Manatee Rivers. The seasonal distribution of nitrate-nitrite nitrogen concentrations was very irregular at all stations (figs. 3, 4, 5, and 6). The highest concentrations of nitrate-nitrite nitrogen were recorded in the Hillsborough River, at station 29 (table 2). The Alafia and Little Manatee Rivers showed higher values at upstream than at downstream stations.

Concentrations of total dissolved copper in all rivers varied from 0.00 to 0.22 μg.at./l. The monthly copper values were very irregular at all stations. The Little Manatee River showed the highest average copper level for the investigation period (table 2). The highest values (0.22 and 0.16 μg.at./l.) were observed at station 31 in the Alafia River during December when copper values for five other stations were low. Except in the case of the Alafia River, slightly higher concentrations of copper were observed at the upstream stations (table 2).

TABLE 1.—*Total phosphorus and inorganic phosphate in Tampa Bay and tributaries, October 1958–December 1959*

[Units in μg.at./l.]

Location	Total PO_4 P			Inorganic PO_4 P		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Hillsborough River:						
Station 29:						
Surface	3.9	8.3	5.8	2.7	7.9	4.9
Bottom	3.4	18.6	10.3	2.6	16.6	8.3
Station 30:						
Surface	2.5	13.9	6.1	2.7	7.4	4.7
Bottom	2.5	10.4	7.1	2.5	7.2	5.7
Alafia River:						
Station 31:						
Surface	20.3	55.8	38.8	19.7	51.2	33.5
Bottom	18.1	58.1	39.2	19.7	55.8	32.3
Station 32:						
Surface	25.0	58.1	39.7	20.2	46.9	34.9
Bottom	24.1	60.5	39.1	21.4	44.8	32.2
Little Manatee River:						
Station 33:						
Surface	8.2	19.8	13.0	6.9	18.6	12.3
Bottom	7.9	21.0	14.9	6.3	20.1	13.0
Station 34:						
Surface	7.0	16.5	10.9	5.3	13.8	9.7
Bottom	6.7	16.8	11.4	5.5	13.7	9.2
Manatee River:						
Station 35:						
Surface	4.7	13.0	10.1	5.9	10.9	8.4
Bottom	8.1	13.2	10.3	6.0	13.0	8.6
Station 36:						
Surface	8.6	19.6	11.9	7.7	18.0	10.1
Bottom	8.8	18.4	11.8	8.1	15.5	10.3
Tampa Bay, off mouth of Little Manatee River:						
Station 3 (27°41.6′ N., 82°33.5′ W.):						
Surface	15.1	33.2	23.3	15.1	29.6	21.0
Bottom	15.9	25.6	19.2	13.1	22.9	17.6
Station 4 (27°41.3′ N., 82°32.9′ W.):						
Surface	16.6	27.1	22.1	14.5	25.8	20.2
Bottom	16.0	26.7	21.6	12.5	23.2	18.2

TABLE 2.—*Concentrations of nitrate-nitrite nitrogen and total dissolved copper in Tampa Bay tributaries, October 1958–December 1959*

[Units in μg.at./l.]

Location	NO_3-NO_2N			Cu		
	Minimum	Maximum	Mean	Minimum	Maximum	Mean
Hillsborough River:						
Station 29:						
Surface	1.1	13.7	7.0	0.02	0.07	0.04
Bottom	0.8	11.2	5.2	.02	.09	.04
Station 30:						
Surface	.7	10.8	4.6	.02	.09	.05
Bottom	.9	12.2	4.7	.02	.08	.04
Alafia River:						
Station 31:						
Surface	.4	9.3	3.9	.02	.16	.06
Bottom	.4	8.8	3.6	.03	.22	.06
Station 32:						
Surface	1.0	11.3	5.5	.02	.08	.05
Bottom	0.7	11.2	5.1	.01	.08	.04
Little Manatee River:						
Station 33:						
Surface	.1	1.3	0.7	.03	.13	.07
Bottom	.1	1.6	0.8	.02	.12	.06
Station 34:						
Surface	.3	2.7	1.0	.02	.12	.08
Bottom	.3	2.6	1.2	.02	.13	.08
Manatee River:						
Station 35:						
Surface	.4	6.8	1.2	.02	.11	.06
Bottom	.3	2.2	0.9	.02	.15	.06
Station 36:						
Surface	.1	2.7	1.1	.00	.16	.05
Bottom	.2	3.6	1.3	.01	.13	.04

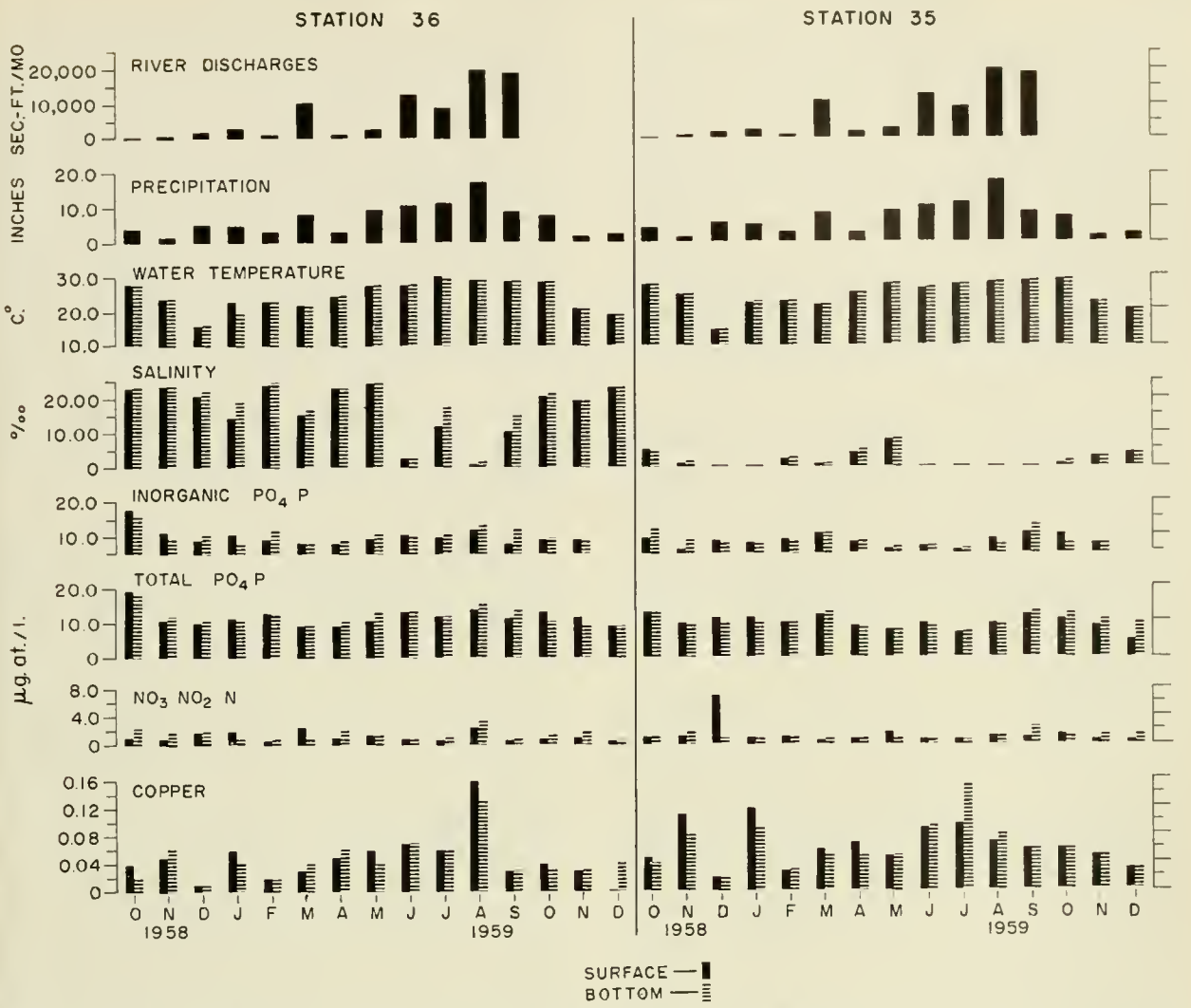

FIGURE 6.—River discharge, precipitation, and hydrological properties of Manatee River, Florida, October 1958–December 1959.

DISCUSSION

The annual temperature range of 15.0° to 30.5° C. observed for Tampa Bay tributaries is comparable to ranges of the shallow coastal subtropical waters at Naples, Florida (Dragovich, 1961), and to bay waters of Texas (Collier and Hedgpeth, 1950). Rapid changes in water temperature during the winter are of considerable significance to the resident biota. Sudden cold spells may result in fish mortalities (Springer and Woodburn, 1960) or influence spawning and migrations in estuaries (Collier and Hedgpeth, 1950).

In general there was a rather good relation between monthly precipitation and river discharges.

Only two river stations, 30 and 34, had fresh-water salinity values (<0.5 ‰) throughout the entire period of investigation. At the remaining stations the salinity levels ranged from oligohaline (0.5 ‰ to 5 ‰) and mesohaline (5 ‰ to 18 ‰) to polyhaline (18 ‰ to 30 ‰). The influence of precipitation was obvious, particularly at stations 29, 31, 32, 33, and 35. The salinity distribution at these stations indicated an alternation between brackish- and fresh-water environments. This condition presents ecological barriers to some organisms from both marine and fresh-water ends of the estuary. In this regard *G. breve*, the Florida red-tide organism, was never found at

stations 29, 31, 33, and 36 even when a red-tide outbreak occurred in lower Tampa Bay and offshore areas. In view of the *G. breve* salinity tolerance findings of Aldrich and Wilson (1960), it seems probable that even the maximum salinity (24.83 ‰) noted at these stations was too low to permit growth of this organism. Low concentrations of *G. breve* (up to 13 per ml.) were observed in samples taken near Bradenton during the red-tide outbreak in 1957. Salinity values for these positive samples were somewhat higher: 25.73 ‰ to 29.27 ‰ (Dragovich and others, 1961).

The distribution of total and inorganic phosphate-phosphorus in the rivers demonstrates the influence of underlying phosphatic formations. Higher concentrations of total and inorganic phosphate were recorded in the Alafia, Little Manatee, and Manatee Rivers which flow through a phosphatic district than in the Hillsborough River which has less contact with natural phosphate deposits.

In contrast to the scarcity of phosphorus in the oceans (Harvey, 1957; Sverdrup, Johnson, and Fleming, 1946), an abundance of this important nutrient element was found in all rivers flowing into Tampa Bay. On the basis of in vitro work (Ketchum, 1939), the concentrations observed represent a more than adequate supply for phytoplankton growth. A sizable contribution of total phosphorus to the waters of Tampa Bay is evident from data presented in table 1. A parallel investigation in Tampa Bay (Dragovich and others, 1961) has shown that upper Tampa Bay waters are richer in phosphorus than all Bay tributaries with the exception of the Alafia River (table 1). The Alafia River contributes the largest quantities of phosphorus to Tampa Bay. Graham, Amison, and Marvin (1954), in their phosphorus studies of the Caloosahatchee and Peace Rivers, observed a high average concentration (12.0 μg.at./l.) of total phosphorus in the Peace River. This value was less than one-third that of the Alafia. Average concentrations of inorganic (1.21 μg.at./l.) and total phosphorus (2.63 μg.at./l.) in the Caloosahatchee River are very low if compared with the corresponding values for any of the rivers flowing into Tampa Bay.

High concentrations of total phosphorus in the rivers were due largely to inorganic phosphate, which represented 77 to 95 percent of the total. Inorganic and total phosphorus were higher at the stations nearer the Bay than at the upstream stations, except in the Alafia River. From figure 7 it is apparent that the maximum concentrations of total phosphorus at station 29 were observed near the bottom and at highest salinities. The difference in total phosphorus values for the surface and bottom at station 33 appears to be insignificant. A phosphorus-salinity relation at stations 31 and 36 is not apparent. However, at station 31 phosphorus values at the few high-salinity levels noted were well below those observed at low salinities. The maximum total phosphorus values at station 36 (fig. 7) cannot be regarded as representative, for the samples were extremely rich in particulate matter.

Maximum concentrations of inorganic and total phosphorus in the Alafia River were recorded during the rainy season at the period of maximum discharges. In the Hillsborough River, where highest river discharges were recorded, a moderate surface increase in inorganic and total phosphorus was observed from March to September at both stations. This pattern was not evident in the Manatee River and the Little Manatee River data. High concentrations of organic phosphorus observed in the Alafia River from May to October may indicate increased biological activity.

In contrast to the high concentrations of phosphorus, the nitrate-nitrite nitrogen observed for these rivers can be considered moderate or low. The distribution of nitrate-nitrite nitrogen observations for all stations (fig. 8) clearly shows the existence of higher concentrations in the Hillsborough and Alafia Rivers than in the Little Manatee and Manatee Rivers. This pattern is similar to that of river discharges. The concentrations of nitrate-nitrite nitrogen in the Hillsborough and Alafia Rivers are comparable to the surface concentrations in certain marine areas such as the Gulf of Maine (Rakestraw, 1936), English Channel (Cooper, 1937), or Arabian Sea off Calcutta (Panikkar and Jayaraman, 1953), while the concentrations in the Little Manatee and Manatee Rivers, if compared to the same areas, are extremely poor. The seasonal distribution of nitrate-nitrite nitrogen and its short-term response to river discharge variation were very irregular.

The mean concentrations of nitrate-nitrite nitrogen in the Hillsborough and Alafia Rivers are

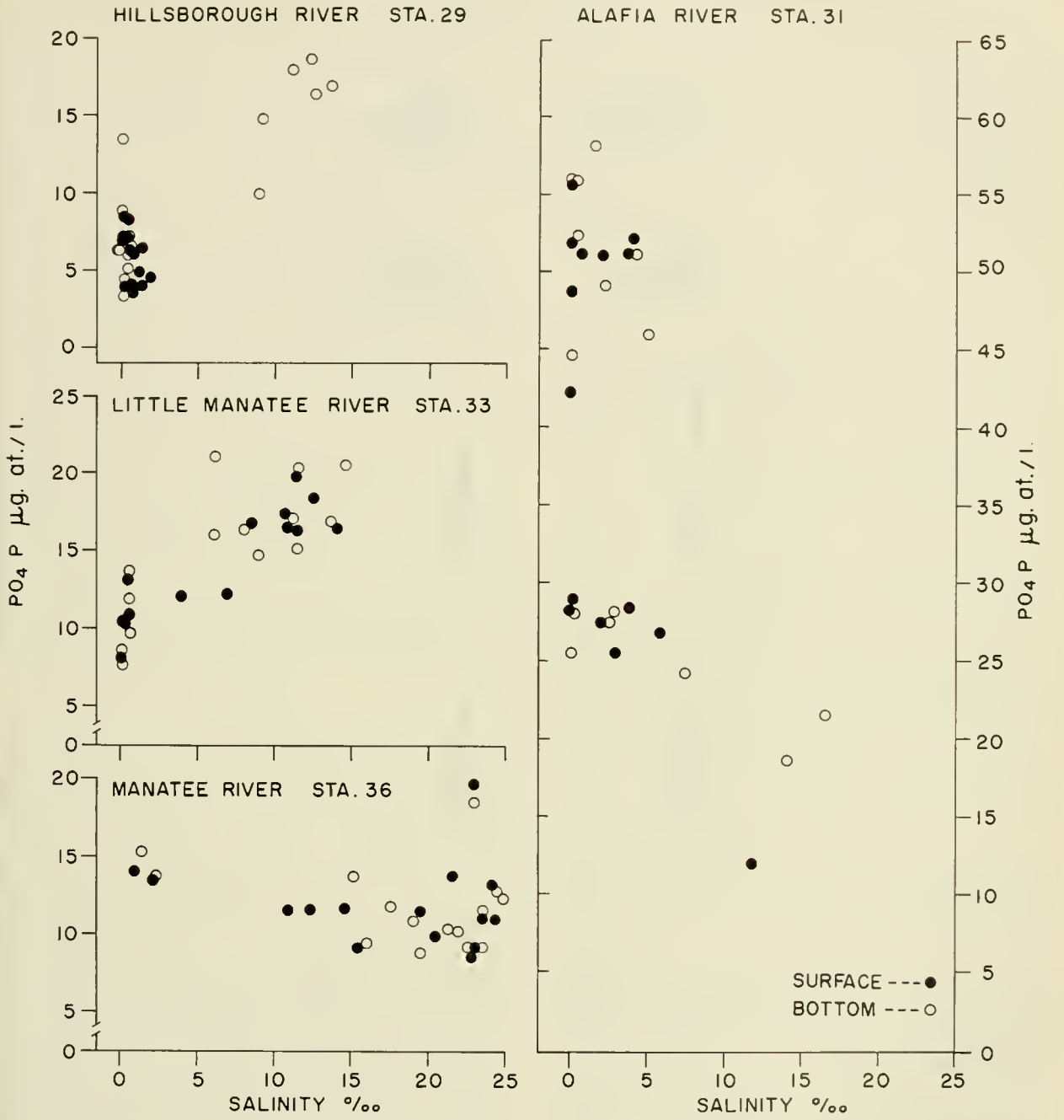

FIGURE 7.—Phosphorus-salinity relation of Tampa Bay tributaries, October 1958–December 1959.

comparable to the mean value (4.7 µg.at./l.) for the Peace River and higher than that for the Caloosahatchee River (2.2 µg.at./l.) (Finucane and Dragovich, 1959). The Little Manatee and Manatee Rivers were even poorer than the Caloosahatchee River in nitrate-nitrite nitrogen. None of these Florida rivers approach the Mississippi River level (14.6 µg.at./l.) for this nutrient (Riley, 1937).

The present data for the rivers, together with parallel observations in Tampa Bay (Dragovich and others, 1961), suggest that the rivers do not enrich the waters of Tampa Bay to an appreciable degree with nitrate-nitrite nitrogen. Dragovich

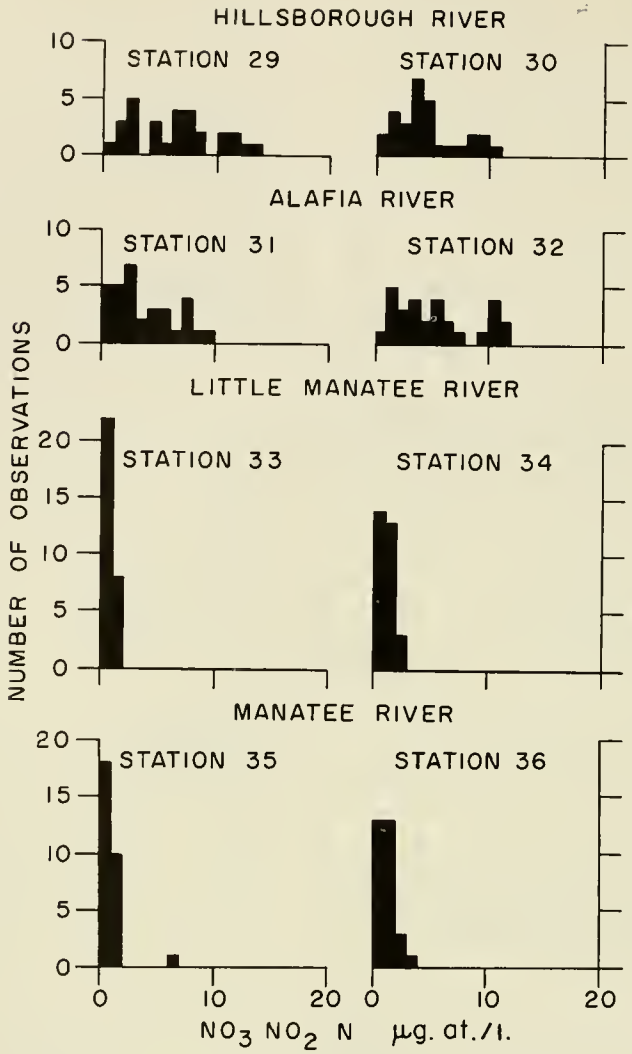

FIGURE 8.—Distribution of nitrate-nitrite nitrogen for rivers flowing into Tampa Bay, October 1958–December 1959.

and others (1961) have shown an extremely low mean concentration of nitrate-nitrite nitrogen (0.3 µg.at./l.) for Tampa Bay during the period of the present study.

Higher nitrate-nitrite concentrations near the Bay than at the upstream stations of the Hillsborough River suggested that enrichment of this river might be from waters somewhere between stations 29 and 30. To check this possibility our observations were extended in October, November, and December 1959 to Sulphur Springs, an underground tributary, located between stations 29 and 30. Nitrate-nitrite nitrogen concentrations in these springs varied from 11.1 to 17.0 µg.at./l., with a mean value of 13.5 µg.at./l. which is comparable to the maximum value observed at station 29. These results suggest that enrichment in nitrate-nitrites at station 29 is partially attributable to these springs.

The copper concentrations in Tampa Bay and adjacent neritic waters for the period from October 1958 through December 1959 varied from 0.00 to 0.10 µg.at./l. with an average of 0.03 µg.at./l. (Dragovich and others, 1961). Thus the mean copper concentration of Tampa Bay is about half of that observed in the rivers.

Copper is generally considered to be an essential constituent of protoplasm, especially in the synthesis of haemocyanin, haemoglobin, cytochrome *a*, and certain metalloflavoproteins (Mahler, 1956). Copper is taken up by phytoplankton (Atkins, 1953). The concentrations of copper in

tissues of certain soft marine invertebrates are about 5,000 times greater than the concentrations observed in the sea (Bieri and Krinsley, 1958; Krumholz and others, 1957). On the other hand, this element is selectively toxic to some organisms, including some algae, barnacles, and gastropods. Laboratory experiments demonstrated that the minimum dissolved copper lethal to *G. breve* in blooming proportions is about 0.5 μg.at./l. (Wilson).[1] Results of this investigation have shown that the average concentration of copper for all rivers combined is well below the toxic levels for *G. breve*. The frequency distribution of copper shows that in 75.6 percent of all observations the concentrations ranged from 0.03 to 0.08 μg.at./l.

The copper concentrations (0.04 μg.at./l.) tabulated by Chow and Thompson (1952) in the low-salinity waters off the mouth of the Mississippi River are comparable to the concentrations observed in the Hillsborough River but are below those observed in the other rivers. The copper levels in all four rivers were higher than those observed in the San Juan Channel, Washington (Chow and Thompson, 1954).

SUMMARY

The estuarine portions of the four main Tampa Bay tributaries can be characterized as subtropical areas subject to considerable variations in several ecologically important factors. These waters seem to be strongly influenced by local precipitation and natural phosphate deposits.

Temperature, salinity, total and inorganic phosphate-phosphorus, nitrate-nitrite nitrogen, and copper were determined monthly for the four main Tampa Bay tributaries. The temperature variations were characterized by rapid changes during the winter and thermal homogeneity from May to October. Salinity was markedly reduced during months of heavy rainfall and river discharges. High phosphate levels were observed in all four rivers. Their drainage areas are rich in natural phosphatic deposits. Extremely high concentrations of phosphate-phosphorus observed in the Alafia River exceeded those in upper Tampa Bay. In the three remaining Tampa Bay tributaries, the concentrations of phosphate-phosphorus were lower than those observed in upper Tampa Bay. Higher concentrations of nitrate-nitrite nitrogen were noted in the Hillsborough and Alafia Rivers than in the Little Manatee and Manatee Rivers. The nitrate-nitrite nitrogen data indicate that rivers do not enrich the waters of Tampa Bay to an appreciable degree. Concentrations of copper averaged twice those observed in Tampa Bay.

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ACCUMULATION AND RETENTION OF CESIUM^{137} BY MARINE FISHES

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The problem of fishes being polluted by radioactive materials released into the aquatic environment [1] becomes increasingly important with the continued development of atomic energy. A major source of pollution has been the detonation of nuclear weapons which released large quantities of radionuclides into the environment (Revelle and Schaefer, 1957). These have made a negligible contribution to the total radioactivity of the sea, but have temporarily contaminated the test areas (Kawabata, 1955; Donaldson and others, 1956; Seymour and others, 1957). There is also a possibility that the oceans may be used for the disposal of concentrated radioactive wastes from the increasing number of atomic reactors (Revelle and Schaefer, 1957). This possibility, along with the testing of nuclear weapons and the present dumping of low-level wastes, emphasizes the need for evaluation of hazards to man through fisheries. Such an evaluation can be made only with a knowledge of the disposition of these radionuclides in the biology of marine organisms.

Radioactive Cs is readily accumulated in the tissues of animals and is therefore a hazard to man when it is released into a marine environment containing animals used as food. Krumholz (1956) found that about 75 percent of the radioactivity in soft tissues of bluegills and crappies in a contaminated lake resulted from Cs^{137}. Suckers in the Columbia River accumulated substantial amounts of this radionuclide in muscle (Davis and others, 1958). Small amounts of Cs^{137} were found in fish muscle, marine algae and fish-eating birds during a resurvey of two atolls of the Marshall Islands approximately 1 year after "Operation Castle" (University of Washington, 1955). Pendleton and Hanson (1958) followed the accumulation of Cs^{137} through food chains in aquatic environments. They reported that carnivorous vertebrates had higher concentration factors than omnivores. Working with invertebrates, one of the authors, T. J. Price (unpublished data), found that clams and oysters concentrated Cs^{137} six times over that by sea water in 20 days, whereas muscle of scallops had a concentration factor of 10 in 10 days.

The metabolism of radioactive Cs by domestic and laboratory animals has been studied by various workers. Weeks and Oakley (1955) fed rats regularly with Cs^{137} as an inorganic solution, biologically incorporated in plant material, and mixed with plant material. Their results indicated that absorption was not affected by the form in which it was fed and that the greatest accumulation occurred in muscle. While studying the metabolism of Cs^{137} in rats, cattle, sheep, swine, and chickens, Hood and Comar (1953) found a high degree of absorption of ingested Cs^{137}, long-term retention and similar concentration patterns among species and among tissues. Ballou and Thompson (1958) administered Cs^{137} to rats both in single doses and over a long period. They found that predictions of the long-continued buildup, based on single dose data, were in close agreement with the results from the prolonged feeding experiment.

The present experiments were undertaken to follow the accumulation of Cs^{137} by fish, both from sea water and from ingested doses; and to determine its biological half-life ($t_{\frac{1}{2}}$), which is the time required for an organism or tissue to lose one-half of a given substance by biological elimination.

METHODS AND MATERIALS

Fish were collected in the vicinity of Beaufort, N.C., and included the following species: postlarval summer flounder, *Paralichthys dentatus* (Linnaeus), weighing 17.6–48.6 milligrams; Atlantic croaker, *Micropogon undulatus* (Linnaeus),

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34–204 grams; bluefish, *Pomatomus saltatrix* (Linnaeus), 250–350 grams and little tuna, *Euthynnus alleteratus* (Rafinesque), 5.4–6.1 kilograms. Fish were weighed immediately prior to radioactivity measurements. Flounder were kept in small indoor tanks and fed nauplii of the brine shrimp, *Artemia salina*. Croaker, bluefish, and little tuna were kept in large outdoor tanks and all except little tuna were fed cut fish. The latter would not accept food while in captivity, and the only experiment utilizing this species was limited to 8 days.

The carrier-free Cs^{137} used in the present experiments was obtained in the form of CsCl in 0.12N HCl from the Oak Ridge National Laboratory, Oak Ridge, Tenn. It has a half-life of 30± 3 years and is in secular equilibrium with Ba^{137}, which has a half-life of 2.6 minutes.

EXPERIMENTAL PROCEDURE

Fish accumulate radioactive Cs by direct absorption from the water and by ingestion of food and water. Both pathways were followed in the present experiments. Radioactivity absorbed by tissues of fish kept in standing sea water containing a given concentration of Cs^{137} was measured (radioassayed) periodically. To determine the amount of absorption from the digestive tract, Cs^{137} was administered orally to fish which were kept in flowing sea water and radioassayed periodically.

Accumulation by absorption from sea water was followed in flounder and croaker. The water was first filtered through cotton to remove particles which might take up Cs^{137}. Frequent radioassay and renewal of the water insured a minimum variation of the Cs^{137} content and prevented a buildup of excretory products. The water was aerated and had an average salinity of $32\pm3°/_{oo}$. Twenty-nine flounder were kept in a battery jar containing 5 liters of sea water with a Cs^{137} concentration of 0.1 μc per ml. The jar was placed in a bath of flowing sea water to maintain a temperature within the range of that in the natural environment. During the experiment the temperature gradually increased from 8° to 18° C. Twenty-four croaker were kept in a tank containing 48 liters of sea water with

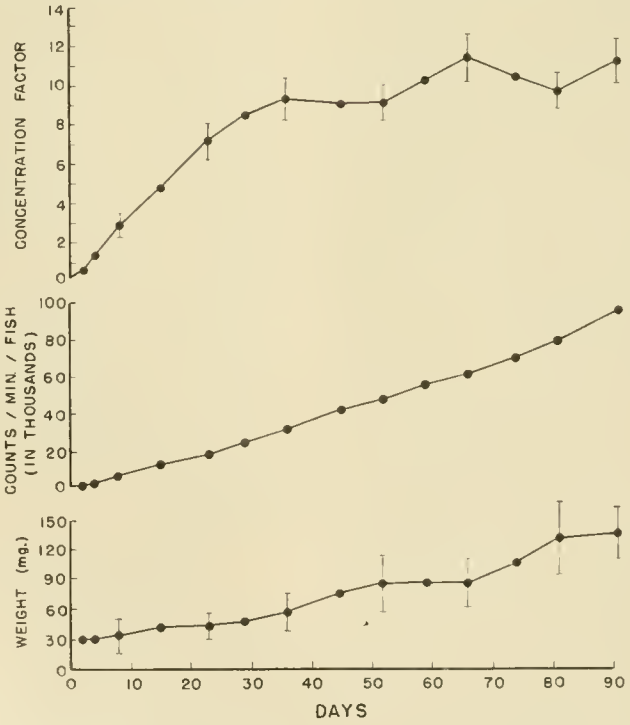

FIGURE 1.—Accumulation of Cs^{137} by postlarval flounder from sea water as influenced by growth rate. Upper curve is based on the ratio of radioactivity in fish to that in an equal weight of water. Center curve is based on radioactivity per individual. Lower curve represents mean weight of fish. Vertical lines are one standard deviation above and below curve.

a Cs^{137} concentration of 0.0005 μc per ml. and a temperature of $21 \pm 1°$ C.

The method selected for administering Cs^{137} orally was that most easily adapted to the particular species of fish. When croaker were used, the radionuclide was pipetted directly into the stomach. However, bluefish regurgitated the liquid, so each dose was changed to a solid by the following method: One-tenth ml. of the radionuclide was pipetted on a small piece of aluminum foil. Into this droplet powdered gelatin was sprinkled until it appeared dry on the surface. The foil was placed on a hotplate set at low heat until the preparation became clear. It was then removed from the hotplate, allowed to dry for about 4 hours and the dose was peeled from the foil and rolled into a cylinder. After drying overnight the dose became quite hard and was introduced into the esophagus of a bluefish by the use of forceps. Because of the extremely large mouth and throat of little tuna, the gelatin doses were first inserted into the body cavity of the pinfish, which in turn were fed to the little tuna by the use of forceps. The amount of Cs^{137} given varied from 0.4 to 1.0 μc per gram of fish. Since the Cs^{137} administered to fish was greatly diluted from the acid stock solution and the volume of each dose was only 0.1 ml., the pH of the contents of the fish stomachs was not significantly affected.

In measuring the Cs^{137} content of postlarval flounder, each fish was rinsed in a screw-cap vial containing 2 ml. of nonradioactive sea water, weighed, and radioassayed alive. By following this procedure it was possible to radioassay all of the flounder at each time interval.

Measurements of radioactivity in croaker or bluefish were averaged from four or five individuals per time interval, but only one little tuna was measured because of the difficulty in keeping a sufficient number alive. After careful dissection, small portions of certain tissues were excised from the same relative positions in all fish. These were placed in screw-cap vials, weighed on a precision balance and radioassayed. Blood samples were taken from the truncus arteriosus with a hypodermic syringe after first making an incision to expose the heart. In some instances both blood serum and whole blood were measured. Separation of the cells from the serum was accomplished by centrifuging the coagulated blood.

RADIOASSAY OF TISSUES

Gamma ray emission of tissues was measured with a well-type scintillation crystal in which 0.01 μc of Cs^{137} yielded a rate of 6,500 counts per minute. Counting rates were not influenced by biological separation of Cs^{137} and Ba^{137} since the short half-life of Ba^{137} permitted the return of secular equilibrium before the samples were radioassayed. All measurements were of required duration to insure a maximum standard deviation of 2 percent. Decay corrections were applied only when experiments exceeded 90 days. In accumulation experiments measurements of Cs^{137} are expressed either in counts per minute per unit weight of tissue, or as a concentration factor, the ratio of radioactivity in fish tissue to the radioactivity in sea water on a unit weight basis. When Cs^{137} was administered orally, all fish of a group were given the same quantity, and measurements of radioactivity in the tissues were corrected to a fish of standard weight. In retention experiments, measurements are expressed as percentages of the radioactivity present at zero time. All values are presented as averages.

RESULTS

ACCUMULATION

Accumulation of a radioactive substance by an organism occurs when the rate of uptake exceeds the rate of excretion. As stated previously, fish in the marine environment may accumulate Cs^{137} directly from sea water or from ingested food. Absorption through both pathways may occur either simultaneously or at different times, depending on the food habits or migratory patterns of the fish concerned. In the present experiments, absorption was followed through the two pathways independently so comparisons could be made between them.

Accumulation from sea water

Whole-body accumulation of Cs^{137} from sea water by postlarval flounder was followed during a period of 91 days. The experiment was begun with 29 fish, but the number was reduced to 24 by mortality during the first 14 days. One additional fish died during the remaining 77 days. The rate of accumulation was fairly uniform during the first 30 days (fig. 1). From the 30th to the 50th day the rate leveled off at a concentration factor of 9, accompanied by a slight increase

in the average weight of the flounder. During the following 14-day period the amount of food given was reduced by approximately one-half. This resulted in a leveling off of the weight curve with a corresponding increase in Cs^{137} accumulation to a concentration factor of 11. When regular feeding was resumed and the average weight increased from the 64th to the 77th day, the Cs^{137} concentration in the fish actually decreased. Results during the final 14 days of the experiment were similar to those found during the period from the 50th to the 63d day.

The reduced rate of accumulation of Cs^{137} per unit weight during periods of rapid weight increase probably was the result of the fish increasing in mass more rapidly than Cs^{137} was accumulated. That is, the amount of Cs^{137} accumulated by new tissue was so small that the increase of radioactivity due to growth was not detectable, as indicated by the middle curve in figure 1, produced by plotting the radioactivity per fish rather than per unit weight. The result was, in effect, a "biological dilution" of the isotope. During periods of slow weight increase the opposite effect was evident apparently because the rate of accumulation exceeded the rate of weight increase.

Accumulation of Cs^{137} by muscle, liver, heart and spleen of croaker was followed during a period of 29 days, the last three tissues being grouped for each determination. Muscle accumulated the radionuclide at a uniform rate, reaching a concentration 4.5 times that of sea water after 29 days (fig. 2). Accumulation occurred more rapidly in liver, heart, and spleen than in muscle, but the rate decreased as the experiment progressed. These tissues had a concentration factor of 9 at the end of 29 days.

Accumulation from the digestive tract

Accumulation and tissue distribution of Cs^{137} by croaker following oral administration of single doses was determined over a 4-day period. Values were based on averages of four fish per time interval. Six hours after the dose was given only 15.4 percent remained in the digestive tract (table 1). The fact that the intestine did not contain more than 5 percent of the dose at any time plus the early appearance of the radionuclide in the organs and tissues indicated rapid absorption. Hood and Comar (1953) reported similar high absorption of Cs^{137} through the rumen walls of cattle.

Tissue concentration of Cs^{137} in the croaker dosed orally (fig. 3) was similar to that in croaker immersed in radioactive sea water. In both experiments, internal organs had rapid rates of accumulation initially, while muscle tissue had a slower rate. However, in the experiment in which croaker were kept in radioactive sea water, a constant supply was available, so that the

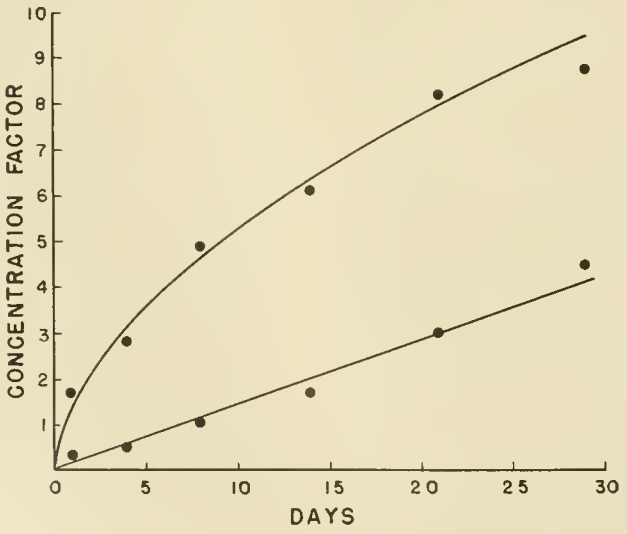

FIGURE 2.—Accumulation of Cs^{137} by croaker from sea water.
Upper curve: heart, spleen, and liver.
Lower curve: muscle.

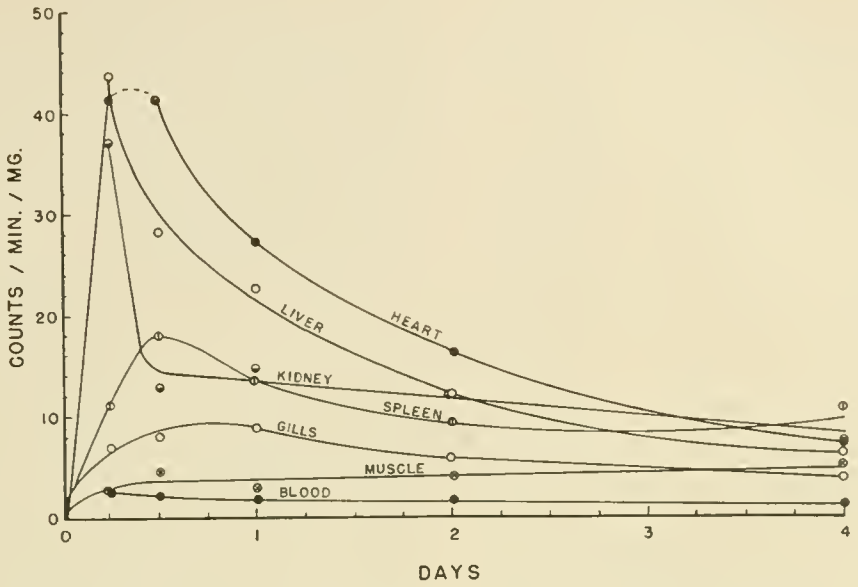

FIGURE 3.—Concentration of Cs^{137} in tissues of croaker following a single oral dose.

amount of Cs^{137} in the organs did not diminish. In the present experiment, the supply of Cs^{137} was limited by a single dose in the digestive tract. Consequently, instead of maximum levels of activity being maintained in the tissues, peaks of concentration were reached at certain time intervals following ingestion.

TABLE 1.—*Cs^{137} remaining in digestive tracts of croaker at intervals following oral administration*

Organ	Percent of dose remaining after—					
	0 day	¼ day	½ day	1 day	2 days	4 days
Stomach	100	7.1	6.2	6.1	3.5	2.3
Pyloric caeca	0	3.3	1.5	0.9	0.8	0.4
Intestine	0	5.0	3.1	2.3	2.1	1.4
Total	100	15.4	10.8	9.3	6.4	4.1

All tissues tested concentrated Cs^{137} to higher levels than blood, which maintained a relatively low and slowly decreasing concentration of the radionuclide. This decrease of radioactivity in the blood probably was an indication of excretion by all tissues tested, since blood serves as a transporting medium for them. The early accumulation by liver, kidney, heart, and spleen, along with the rapid loss from the digestive tract, indicates that the internal organs concentrated most of the radionuclide as soon as it became available in the blood. The accumulation of Cs^{137} by the gills was high during the first few hours, but leveled off and began to decrease 24 hours after dosage. Muscle, after an initial brief period of rapid uptake, accumulated the radionuclide at a slower but uniform rate while the available Cs^{137} became reduced in the digestive tract and the other tissues.

Accumulation and tissue distribution of Cs^{137} in little tuna from a single oral dose were followed during an 8-day period. As in the croaker, the internal organs took up the radionuclide at a fast rate, concentrating it over levels in the blood; muscle and gonad had slower rates and moderate levels of concentration, while the other tissues had relatively low concentrations (table 2). It is interesting that on the first day 99 percent of the Cs^{137} in the blood was located in the serum, while on the sixth day only 44 percent was in the serum and 56 percent in the cells.

The tissue distribution of Cs^{137} in bluefish was determined 24 hours after oral administration. The results of this test were generally similar to those found for croaker and little tuna (table 3).

TABLE 2.—*Concentration of Cs^{137} in different tissues of little tuna following a single oral dose*

Tissue	Counts/minute/mg. after—			
	1 day	3 days	6 days	8 days
Liver	4,761	2,473	1,813	1,358
Heart	3,214	1,652	1,322	821
Spleen	1,848	1,728	1,692	821
Kidney	1,643	1,356	932	499
Blood, whole	324	230	205	----
Blood serum	322	145	90	----
Muscle	241	352	457	403
Gonad	285	366	699	705
Bone	212	209	90	137
Eye	159	134	163	158
Brain	155	182	362	347
Skin	154	242	216	531

TABLE 3.—*Relative concentration of Cs^{137} in tissues of three species of marine fish 1 day after a single oral dose*

Tissue	$\frac{\text{cpm/unit wt. tissue}}{\text{cpm/unit wt. blood}}$		
	Croaker	Bluefish	Little tuna
Blood	1.0	1.0	1.0
Liver	12.5	5.9	14.6
Spleen	7.5	6.4	5.6
Kidney	8.0	4.9	5.1
Gonad	2.4	1.8	.9
Muscle	1.7	1.5	.7
Bone	1.1	1.3	.6
Skin-scales	1.1	.8	.5
Gills	4.9	2.1	----

RETENTION

Experiments were conducted in which whole-body retention of Cs^{137} by postlarval flounder and the retention by certain tissues of croaker were observed. Data were plotted against time on semi-log paper as percentages of Cs^{137} present at zero time and analyzed by the standard kinetic approach usually applied to first-order reactions (Comar, 1955; Richmond, 1958). This procedure need not be discussed here in detail, but a brief description may facilitate presentation of the experimental results.

After fitting the curve to the retention data by inspection, the slope of the linear tail was more accurately determined by the method of least squares and extrapolated back to the y axis or zero time. The extrapolated values were subtracted from the corresponding values of the composite curve, and the differences were plotted on an expanded scale for greater accuracy. The linear tail of the new composite curve was extrapolated in the same manner, and the differences between the extrapolated values and composite values were plotted as before. This procedure was repeated until the final subtraction produced a straight line.

Analysis of the retention process by this method determines the number of exponential functions involved, the rate of removal per unit time by each function, and the amount of substance at zero time represented by each rate function. It is not to be inferred, however, that each function represents removal from a single compartment, since there may be intermediate steps involved or several compartments may be contributing to a single rate function.

TABLE 4.—*Retention of Cs^{137} by postlarval flounder and croaker, showing separation of composite curves into individual rate functions*

Fish and fish tissues	Components of retention curve [1]											
	a_1 percent	k_1 days	$(t_{½})_1$ days	a_2 percent	k_2 days	$(t_{½})_2$ days	a_3 percent	k_3 days	$(t_{½})_3$ days	a_4 percent	k_4 days	$(t_{½})_4$ days
Flounder, whole-body:												
per fish	34	0.1308	5.3	66	0.0188	36.9	----	----	----	----	----	----
per unit weight	67	.1024	6.8	33	.0149	46.4	----	----	----	----	----	----
Croaker tissues, per unit weight:												
Skin	87	.1118	6.2	10	.0265	26.2	3	0.0024	290.0	----	----	----
Muscle	35	.0199	34.8	61	.0073	94.7	----	----	----	----	----	----
Gonad	86	.0517	13.4	3	.0008	911.0	----	----	----	----	----	----
Liver	61	1.0343	.7	37	.1631	4.2	2	.0288	24.1	0.4	$k \doteqdot 0$	$t_{½} \doteqdot \infty$

[1] From the equation $R = a_1e^{-k_1t} + a_2e^{-k_2t} + \ldots a_ne^{-k_nt}$ and $t_{½} = \frac{0.693}{k}$ (Richmond 1958).

The retention process may be expressed by the form $R=a_1e^{-k_1t}+a_2e^{-k_2t}+\cdots a_ne^{-k_nt}$ in which a_1, a_2, . . . a_n and k_1, . . . k_n are the intercept and rate constants, respectively, of the individual or first-order components of the retention or elimination process (Richmond, 1958). Values of k were calculated by multiplying the slope of the line by 2.3, the slope being $(\log A_0-\log A)/t$ in which A_0 represents the amount of material at zero time and A the amount at time t. Biological half-life was determined by the form $t_{½}=0.693/k$ (Comar, 1955).

Whole-body retention

The retention of Cs^{137} by flounder which had accumulated the radionuclide for 3 months was followed over a period of 44 days. Water temperature varied between 22° and 26° C., and the average salinity was 32‰. Twenty-three flounder were radioassayed individually, and the values averaged for each determination. Mortality reduced the number of fish to 13 by the 37th day and to 8 fish by the last day.

The retention curve for postlarval flounder was composed of two exponential rate functions (fig. 4). The first component (A) contained 34 percent of the amount of Cs^{137} at zero time and had a $t_{½}$ of 5.3 days. The second component (B) contained 66 percent of the Cs^{137} at zero time and had a $t_{½}$ of 36.9 days. It is significant that the larger portion of Cs^{137} was represented by the slower moving component. In view of the experiments with croaker described earlier, this larger portion probably represented the influence of muscle. It should be remembered that these fish had been exposed to Cs^{137} for 3 months so there was ample time for a buildup of the radionuclide in muscle. Furthermore, muscle represents the largest mass of any single tissue.

The same data also were plotted on a unit-weight basis. As expected, the results were different because of changes in rate of weight increase (table 4). The first component contained 67 percent of the Cs^{137} at zero time and had a $t_{½}$ of 6.8 days. The second component contained 33 percent of the Cs^{137} and had a $t_{½}$ of 46.4 days. It is interesting to note that the slow-moving component represented the smaller portion. The reason for this difference is that during the period from the 24th to 44th day no significant change in weight occurred, but during the first 23 days

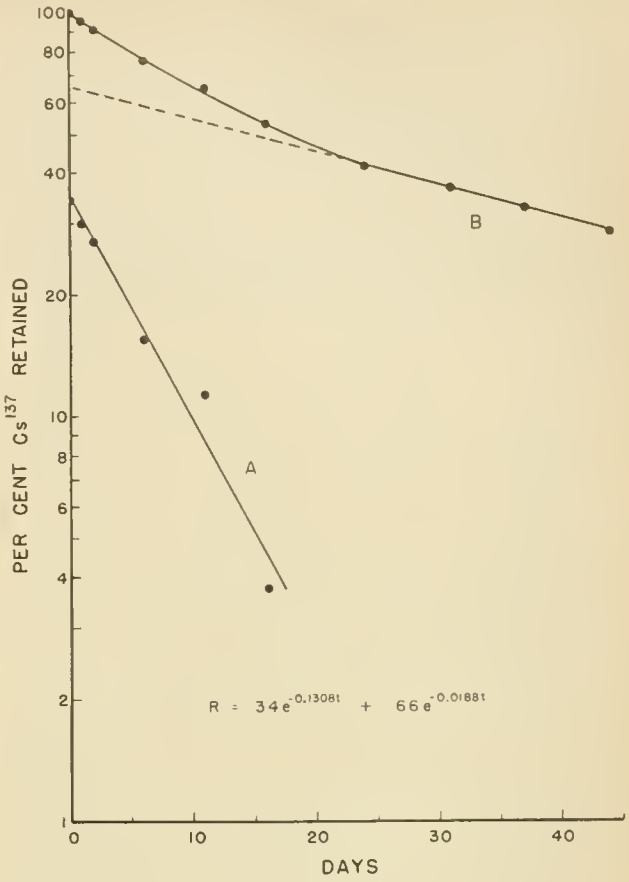

FIGURE 4.—Retention of Cs^{137} by postlarval flounder, showing separation of composite curve into two rate functions.

there was an increase. The weight increase in effect produced an elimination rate largely influenced by "biological dilution" which was not evident in the period from the 24th to the 44th day. This resulted in a slower apparent elimination rate for the second component which indicated a small percentage when extrapolated back to zero time. Undoubtedly, the first curve based on the amount of Cs^{137} per fish presents the more reliable picture of whole-body retention by postlarval flounder.

Tissue retention

Retention of Cs^{137} by selected tissues of croaker following administration of an oral dose was observed over a period of 219 days. The experiment was begun in May and completed in January, so that water temperatures gradually increased from 24° C. to a maximum of 32° C. during August, then decreased to a minimum of 10° C. at the end of the experiment. Salinity

ranged from 30 to 35‰ during the period of observation. Starting 24 hours after dosage, skin, muscle, liver, and gonad of sacrificed croaker were radioassayed periodically, and retention curves were drawn by inspection (fig. 5). These curves were then analyzed and replotted by the methods described above. The curve for skin is presented (fig. 6) as a typical example, and retention data on all the tissues are presented in table 4.

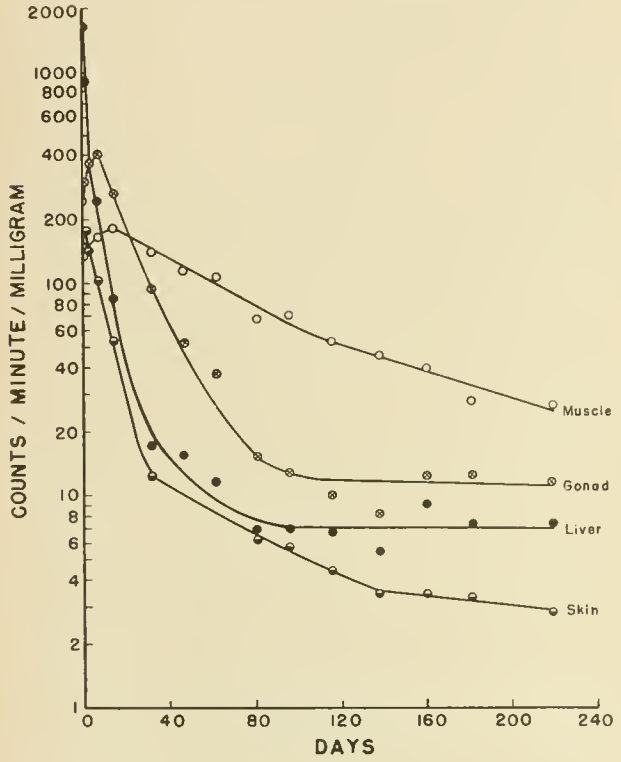

FIGURE 5.—Retention of Cs^{137} by certain croaker tissues following a single oral dose. Curves fitted by inspection.

The concentration of Cs^{137} by skin was relatively low at zero time as compared to the other tissues and decreased rapidly for several days. The retention curve consisted of three rate functions or components with $t_{\frac{1}{2}}$'s of 6.2, 26.2, and 290.0 days (fig. 6). These components represented 87, 10, and 3 percent of the amount of Cs^{137} at zero time.

Muscle continued to accumulate Cs^{137} until the 14th day, which was considered zero time in calculating retention rates. Although the concentration in muscle was relatively low in the beginning, the slow elimination rate resulted in a

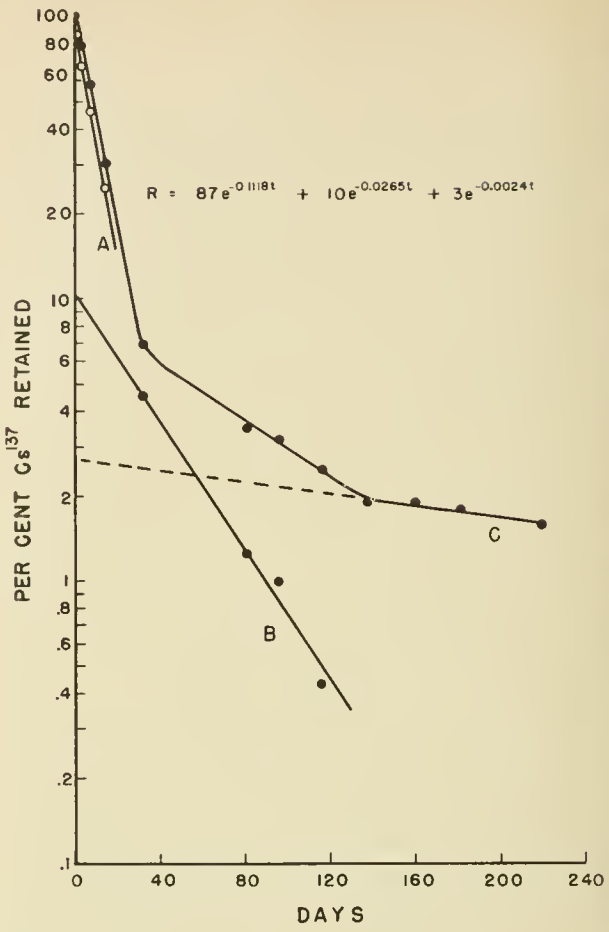

FIGURE 6.—Retention of Cs^{137} by croaker skin, showing separation of a typical composite curve into three rate functions.

relatively high concentration after 219 days. The composite retention curve was resolved into two rate functions with $t_{\frac{1}{2}}$'s of 34.8 and 94.7 days, representing 35 and 61 percent of the amount of Cs^{137} in muscle at zero time. The sum of both components was only 96 percent leaving a deficit of 4 percent which probably was masked by individual variation in samples. The retention of Cs^{137} by rat muscle was expressed as a 2-component curve with $t_{\frac{1}{2}}$'s of 8 and 16 days, representing 55 and 45 percent of the Cs^{137} at zero time (Ballou and Thompson, 1958).

Gonads accumulated Cs^{137} for 7 days before reaching a maximum concentration, which was considerably higher than that of skin and muscle. Although elimination of Cs^{137} was fairly rapid, the concentration remained higher than that of skin and muscle at the end of the experiment.

The retention data were expressed as a composite curve consisting of two rate functions which were extremely different from each other. The first component had a $t_{\frac{1}{2}}$ of 13.4 days, representing 86 percent of the Cs^{137} at zero time. The second component had a $t_{\frac{1}{2}}$ of 911.0 days, representing only 3 percent of the Cs^{137} at zero time. The sum of both components indicated a deficit of 11 percent which denoted either a third rate function not detectable from the data or a masking effect by variation. During the summer months it was noted that the gonads of both males and females discharged ripe sex products. Differences in retention between males and females were not evident from the data. Retention of Cs^{137} by rat ovaries was considerably different from croaker gonads. Ballou and Thompson (1958) reported a 3-component curve with $t_{\frac{1}{2}}$'s of 1.5, 7, and 17 days.

The concentration of Cs^{137} in liver at zero time was much higher than that of the other tissues. However, elimination from liver occurred at a rapid rate, resulting in a lower concentration than that of gonad and muscle after 219 days. The retention curve consisted of four rate functions with $t_{\frac{1}{2}}$'s of 0.7, 4.2, 24.0 and infinite days. The individual components represented 61, 37, 2, and 0.4 percent of the Cs^{137} at zero time. Ballou and Thompson (1958) reported the retention curve for Cs^{137} in rat liver as having three components with $t_{\frac{1}{2}}$'s of 2, 7, and 16 days, representing 69, 19, and 12 percent of the Cs^{137} at zero time.

DISCUSSION

In the present experiments an attempt has been made to reproduce conditions that occur in the natural environment. This approach was used especially in the long-term accumulation experiment with flounder and in both retention experiments.

Accumulation of Cs^{137} by flounder was followed through a temperature range which conformed to the gradual change from winter to spring temperatures in the local estuary. Although the reduction of food at certain times may have produced less than optimum conditions, it is conceivable that fish in their natural environment also tolerate periods of inadequate food supply. The fact that flounder had a higher concentration factor during the period in which they did not increase in weight than during the period in which they did increase may be contrary to what might be expected. However, if Cs is not essential for growth, the amount accumulated would not be proportional, necessarily, to the rate of weight increase.

According to the present results and published reports, Cs concentration factors for most fishes range approximately from 10 to 20, depending upon growth rate, water temperature, and other conditions. Young spot (*Leiostomus xanthurus*) had a concentration factor of 12 for the whole-body, 17 for viscera, and 23 for muscle (George H. Rees, U.S. Bureau of Commercial Fisheries, Beaufort, N.C.; unpublished data). Krumholz and others (1957) gave an approximate factor of 10 for soft tissues of marine vertebrates. Pendleton and Hanson (1958) reported concentration factors of 9,500 and 3,000 for muscle of sunfish (*Lepomis gibbosus*) and carp (*Cyprinus carpio*) in an aquatic community. These factors were based on the amount of Cs^{137} in the water after it had become stabilized at 5 percent of its original concentration, 95 percent having been removed in 50 hours by the ecosystem, including inanimate surfaces. If the same data on sunfish muscle were related to the initial Cs^{137} concentration of the water, they would yield a factor of 8+ which is in closer agreement with the present data.

Accumulation of Cs^{137} from sea water and from ingested material has been followed independently in the present investigation. In certain situations in the marine environment both of these pathways might be utilized simultaneously. In other situations, fish might absorb radioactivity mostly from food due to differences in migratory patterns between fish and their prey. In noncontaminated water, the rate of accumulation of radioactive Cs by fish depends upon the nature of the contaminated food ingested. For example, Pendleton and Hanson (1958) reported higher Cs^{137} concentration factors for carnivorous vertebrates than for omnivores. Fish feeding entirely on phytoplankton might be expected to have even lower concentration factors than omnivorous fish. This is based on data indicating that nine species of algae had concentration factors ranging from 1.2 for *Nitzschia closterium* to 3.1 for *Nannochloris atomus* (Boroughs and others, 1957).

The whole-body Cs^{137} retention curve of flounder consisted of two rate functions with $t_{\frac{1}{2}}$ values of 5.3 and 36.9 days. These are considerably lower rates than those found for clams and oysters, both of which had component $t_{\frac{1}{2}}$'s of 3 and 12 days (T. J. Price, unpublished data). It is pointed out that the muscle to organ ratio of fish is large compared to that of clams and oysters, which may account for the longer $t_{\frac{1}{2}}$ of Cs^{137} in flounder. Richmond (1958) expressed the retention of Cs^{134} in mice, rats, monkeys, dogs, and man as multiple rate function curves. None of the $t_{\frac{1}{2}}$ components for mice or rats exceeded 14 days. The component rate function of monkeys and dogs was more nearly similar to those of flounder, the $t_{\frac{1}{2}}$ values being 3, 23, and 40.5 days for monkeys and 1.1, 27, and 43.5 days for dogs.

The Cs^{134} retention curve for man consisted of two rate functions having $t_{\frac{1}{2}}$ values of 3 and 143 days. McNeill and Green (1959) gave the retention of Cs^{137} in man as a single rate function with an effective half-life of about 115 days. It is likely that the retention curve for flounder might have included a third rate function if it had been possible to continue the experiment. Also it is likely that the long accumulation period prior to the retention experiment might have influenced the characteristics of the retention curve by enabling a greater portion of the Cs^{137} to be concentrated in muscle. This is suggested by the slow rates of accumulation and loss by croaker muscle as compared to the other tissues.

Croaker muscle, with the lowest Cs^{137} concentration at zero time, retained the highest concentration after 219 days of all tissues tested. This was due to the relatively long $t_{\frac{1}{2}}$'s of 34.8 and 94.7 days, both of which were substantial percentages (35 and 61 percent) of the Cs^{137} at zero time. This is significant since muscle represents the greatest mass of tissue. A croaker prepared for the frying pan (less entrails, head, scales, and fins) represents approximately 53 percent of its original body weight; about 5 percent of this is bone, leaving 48 percent edible muscle and skin.

Liver, in contrast to muscle, had an extremely high Cs^{137} concentration at zero time, but 61 percent of this amount had a $t_{\frac{1}{2}}$ of 0.7 day, and 37 percent had a $t_{\frac{1}{2}}$ of 4.3 days. Consequently, the concentration was very low at 219 days.

Although the 911-day $t_{\frac{1}{2}}$ component of gonad and the infinite $t_{\frac{1}{2}}$ component of liver may seem unusually long, there is no indication that they would have remained unchanged with the arrival of summer temperatures. If observations were begun during the winter instead of the summer, one might expect component rate functions somewhat different from those obtained. Therefore, the present values should not be interpreted as fixed values, since they might be influenced by changes in temperature, salinity, food availability, and other factors in the environment.

The authors wish to thank Dr. Earl Deubler, University of North Carolina Institute of Fisheries Research, Morehead City, N.C., for supplying some of the fish used in this investigation, and William S. Davis, for advice on statistical treatment of the data.

SUMMARY

A series of laboratory experiments were performed in which accumulation and retention of cesium^{137} by marine fishes were followed. In order to simulate conditions occurring in a marine environment which might control the availability of the radionuclide, Cs^{137} was administered orally to fish in some experiments while in others the fish were kept in sea water containing known amounts of the radionuclide.

1. Postlarval summer flounder (*Paralichthys dentatus*) concentrated 9 to 11 times the amount of Cs^{137} in sea water during a period of 91 days. The rate of accumulation per unit weight decreased during periods in which the flounder gained weight rapidly. On the other hand, when the flounder did not significantly gain weight, the rate of accumulation increased. This was attributed to the disparity between rate of accumulation and rate of weight increase.

2. Atlantic croaker (*Micropogon undulatus*) concentrated Cs^{137} in heart, liver, and spleen by a factor of 9 times the amount in sea water after 29 days. Muscle accumulated the radionuclide at a slower but more uniform rate with a concentration factor of 4.5.

3. Orally administered Cs^{137} was rapidly absorbed from the digestive tract of croaker with only 10.8 percent of the dose remaining after 24 hours.

4. Maximum concentrations of Cs^{137} occurred in all tissues of croaker, except muscle, within 24 hours following oral administration.

5. Tissue distribution of Cs^{137} was similar in croaker (*Micropogon undulatus*), bluefish (*Pomatomus saltatrix*), and little tuna (*Euthynnus alleteratus*) 24 hours following oral administration, with highest tissue concentrations in the following order: heart, liver, spleen, kidney, gills, gonad, muscle, skin+scales, blood, and bone.

6. Whole-body retention of Cs^{137} by postlarval flounder was expressed as two rate functions with biological half-lives ($t_{\frac{1}{2}}$'s) of 5.3 and 36.9 days representing 34 and 66 percent of the Cs^{137} at zero time.

7. Composite Cs^{137} retention curves of croaker tissue were resolved into multiple rate functions as follows:

Skin—Three rate functions with $t_{\frac{1}{2}}$'s of 6.2, 26.2, and 290.0 days representing 87, 10, and 3 percent of the amount of Cs^{137} at zero time.

Muscle—Two rate functions with $t_{\frac{1}{2}}$'s of 34.8 and 94.7 days, representing 35 and 61 percent of the amount of Cs^{137} at zero time.

Liver—Four rate functions with $t_{\frac{1}{2}}$'s of 0.7, 4.2, 24.1 and infinity representing 61, 37, 2, and 0.4 percent of the amount of Cs^{137} at zero time.

Gonad—Two rate functions with $t_{\frac{1}{2}}$'s of 13.4 and 911.0 days representing 86 and 3 percent of the amount of Cs^{137} at zero time.

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POMPANOS (*TRACHINOTUS* SPP.) OF SOUTH ATLANTIC COAST OF THE UNITED STATES

By HUGH M. FIELDS, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

Three species of the carangid genus *Trachinotus* Lacépède (pompanos), namely, *Trachinotus carolinus* (Linnaeus), *T. falcatus* (Linnaeus), and *T. glaucus* (Bloch), are recognized as being indigenous to the south Atlantic coast of the United States. It is my purpose to present the results of a study of the early development of the pompanos, including descriptions and illustrations of the young, discussion of pigmentation, ontogeny and growth, seasonal occurrence of the young on the Georgia coast, and natural history notes.

The bulk of the *T. carolinus* and *T. falcatus* material used in this study was collected in conjunction with the biweekly seining program of the Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Georgia. (This material is identified in this paper by the abbreviation BLBG.) This program, initiated in 1953 and still in operation, consists of periodic seining at selected sites with small-mesh (¼-inch bar) seines, 30 to 70 feet in length. Three permanent sites are used—open ocean beach (King and Prince, St. Simons Island), salt marsh (Jekyll Island Causeway, and previously, Sapelo Marsh), and fresh-water river (Altamaha River at the county landing). Supplementary seining is done on the open beach at Jekyll Island and at East Beach on St. Simons Island. These seine locations are in Glynn County, Ga., except Sapelo Marsh which is in adjacent McIntosh County, Ga. Water temperature and salinity data are recorded from these sites. Most of the *Trachinotus* taken by seine are from the open ocean beach locations. Other inshore specimens were collected in shrimp trawls in the Brunswick area and by the Menhaden Investigations, Biological Laboratory, Beaufort, N.C., (MI). Offshore specimens were taken during the South Atlantic Fishery Investigations' field operations with the Fish and Wildlife Service research vessel *Theodore N. Gill;* and during operations aboard the Service's exploratory fishing and gear research vessel *Combat. Gill* specimens were collected in plankton tows using standard half-meter silk nets, high-speed metal nets, and by small-mesh dipnets; and the *Combat* material was collected in tows using a standard meter larvae net.

Other specimens examined were lent by the following institutions and individuals:

University of Florida Collections (UF), through John D. Kilby; Charleston Museum (ChM), through E. Milby Burton; United States National Museum (USNM), through Leonard P. Schultz; Institute of Jamaica (Inst. Jam.), through David K. Caldwell; University of Georgia (UG), through Donald C. Scott; Department of Biology, College of Liberal Arts, Boston University (BU), through Robert H. Gibbs; and the personal collection of Mr. and Mrs. Craig Phillips (Phillips). Also examined were fish in the commercial catch at Melbourne and Grant, Fla., on the Indian River, through the courtesy of Floyd Carver and other Indian River fishermen. Appreciation is expressed to the Indian River fishermen and staff members of the Biological Laboratory, Brunswick, Ga., and others who assisted in various ways.

Collection data for all specimens examined are given in appendix table 1, page 210.

METHODS AND DEFINITIONS

Measurements

Measurements below about 15 mm. were made with a micrometer eyepiece and dissecting microscope. Larger measurements were made with dividers and millimeter rule, dial calipers, or measuring board. All measurements below 5 mm. were recorded to the nearest hundredth millimeter; those between 5 and 50 mm. to the nearest tenth; and those above 50 mm. to the nearest half-milli-

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meter. The following measurements were used in this study:

Standard length (S.L.).—The distance, parallel to the longitudinal axis of the body, from the tip of the snout to the distal end of the hypural bones.

Depth.—Shortest distance from insertion of last dorsal spine to insertion of first anal spine.

Head length.—Distance, parallel to longitudinal axis of the body, from tip of snout to posteriormost point of opercular flap.

Eye diameter.—Distance, parallel to longitudinal axis of the head, from anteriormost to posteriormost points of bony orbit.

Dorsal-lobe length.—Shortest distance between insertion of last dorsal spine and distalmost point of dorsal-fin lobe.

Anal-lobe length.—Shortest distance between insertion of third anal spine and distalmost point of anal-fin lobe.

Dorsal-base length.—Shortest distance between insertion of first dorsal spine and insertion of last dorsal soft-ray.

Anal-base length.—Shortest distance between insertion of first anal spine and insertion of last anal soft-ray.

Pectoral length.—Shortest distance between insertion of pectoral-fin spine and distalmost point of pectoral fin.

Pelvic length.—Shortest distance between insertion of pelvic-fin spine and distalmost point of pelvic fin.

Caudal lobe length.—Shortest distance from anteriormost secondary ray of upper caudal lobe to posteriormost point of upper caudal lobe.

Enumerations

Numerable characters used here are dorsal-, anal-, pectoral-, pelvic-, and caudal-fin formulae; gill-raker and preopercular-spine counts; branchiostegal-ray counts; and dentition.

Spines are represented by Roman numerals and soft rays by Arabic numerals. In small fish interspinous membranes are present between the dorsal spines and the anal spines as well as between the posteriormost spines and the anteriormost soft rays. As the fish grows, the interspinous membranes degenerate and the posteriormost spine becomes adnate to the soft fin. Therefore, the posteriormost spine in the dorsal and anal fins is considered part of the soft fin. A specimen bearing a dorsal complement of seven spines and 20 soft rays will have a dorsal formula written VI–I, 20 whether or not the spines are joined by membranes to each other or to the soft fin.

The development of principal caudal rays only is treated here.

Gill-raker counts were taken from the first gill arch. The formula consists of the number of rakers above the one at the angle of the arch plus the angle raker and those on the lower limb, i.e., a gill-raker formula of 7+13 signifies 7 rakers on the upper limb, 1 at the angle, and 12 on the lower limb of the first arch.

Branchiostegal rays, counted on both sides, are recorded left to right, i.e., 8+7 indicates eight rays in the left and seven in the right branchiostegal regions.

Specimens were examined for dentition on the premaxillaries, vomer, palatines, tongue, and dentaries.

All lengths of fish are standard lengths unless otherwise stated.

Growth and Development

In the discussion of growth and development, my findings are compared with those of Ginsburg (1952). The pectoral soft-ray enumerations do not agree with Ginsburg, as his ray counts indicate a minimum and maximum range of one more ray than I found. It is assumed that he included the pectoral spine in his counts, and as presented here the counts exclude the spine.

A soft-ray is considered branched when the cleft separates the distalmost segment into two distinct segments. The uppermost or anteriormost ray of the pectoral fin and the uppermost and lowermost principal rays of the caudal fin never branch. Branching is considered complete when all other rays in these fins have branched, ignoring the branching to the base of the posteriormost ray in the dorsal and anal fins. Branching presents no distinct pattern in the dorsal or anal fins other than that the fourth through last rays usually branch before the first three. The pectoral and pelvic fins branch progressively away from the spine. The median caudal rays branch first, followed by progressive branching of the other principal rays.

Development of body parts is presented as percent of standard length (% S.L.).

Drawings

Drawings were made with the aid of a dissecting microscope and camera lucida.

UNIDENTIFIED LARVAE *Trachinotus*

Six larvae less than 5 mm. long were taken beyond the 100-fathom line during *Gill* and *Combat* operations. Three were so mutilated as to be of little diagnostic use.

The illustrated specimens (figs. 1, 2, and 3) are designated *Trachinotus* primarily on the distinctive shape and arrangement of the preopercular spines and the ontogenetic connection with the development of these spines in slightly larger *Trachinotus*. The 4.66-mm. specimen may well be *T. carolinus*, considering the number of dorsal and anal fin ray buds present and the space left for more buds. The 3.07-mm. specimen resembles the 4.66-mm. larva and may also be *T. carolinus*. The 4.0-mm. larva is so distorted as to resist speculation on its specific identification.

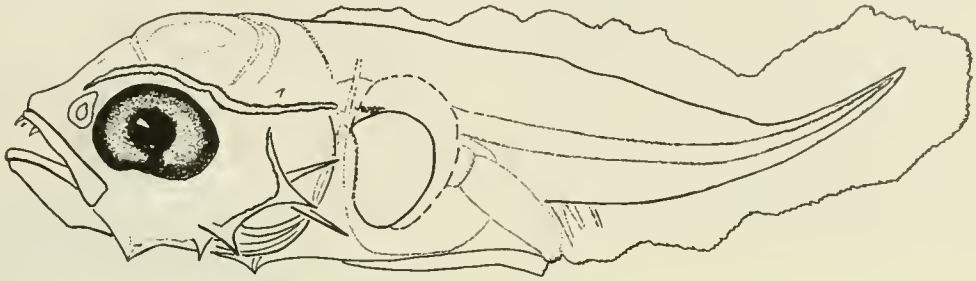

FIGURE 1.—*Trachinotus* sp., 3.07 mm. (*Gill* cruise 2, regular station 2).

FIGURE 2.—*Trachinotus* sp., 4.0 mm. (*Combat* station 302).

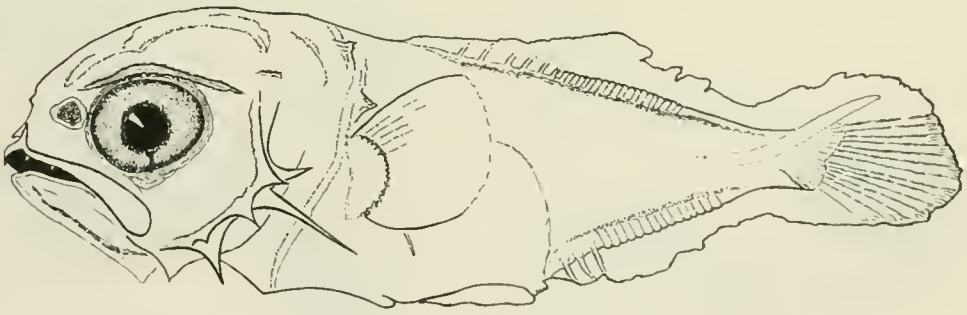

FIGURE 3.—*Trachinotus* sp., 4.66 mm. (*Combat* station 302).

TRACHINOTUS SPP. OF SOUTH ATLANTIC COAST

TRACHINOTUS CAROLINUS (LINNAEUS)

Trachinotus carolinus, (figs. 4–7), the common pompano, is apparently the most abundant species of the genus *Trachinotus* on the southeastern coast of the United States. Meek and Goss (1885: p. 128) stated that "On our South Atlantic and Gulf Coasts this is by far the most abundant species of the genus." Neither Beebe and Tee-Van (1933) nor Bean (1906) included *T. carolinus* among the Bermuda fishes, nor did Rosen (1911) list it for the Bahamas. Nichols (1929: p. 242) stated that the young are plentiful in Porto Rican waters, but grown fish are rare.

The species affords an important fishery along the south Atlantic and Gulf coasts of the United States, with Florida the leading producer. From 1955 through 1958 the total Florida catch was 2,425,247 pounds, valued at $1,748,993 (Anderson and Power, 1957; Bureau of Commercial Fisheries, 1959; Power, 1958 and 1959).

Spawning

There has been considerable speculation on the life history of *T. carolinus*, especially as to time and place of spawning. Goode (1882: p. 39) quoted Stearns, "In regard to its spawning habits nothing very definite has been learned. It has spawn half developed when it arrives and has none when it leaves the bays."

Goode also said (p. 38)—

Mr. S. C. Clarke states that in the Indian River they spawn in March in the open sea, near New Smyrna, Fla. It is supposed that those visiting our northern coasts breed at a distance from the shore.

Tracy (1910: p. 113) stated his belief that *T. carolinus* "probably spawn on east coast of

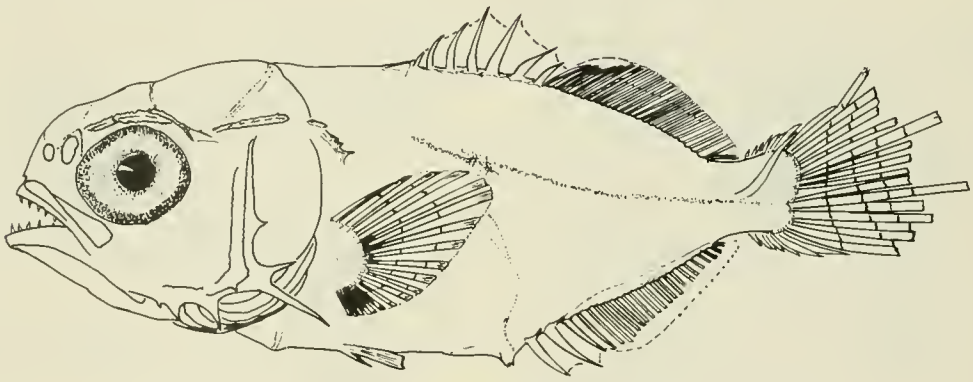

FIGURE 4.—*T. carolinus*, 7.2 mm. (*Gill* cruise 3, regular station 42).

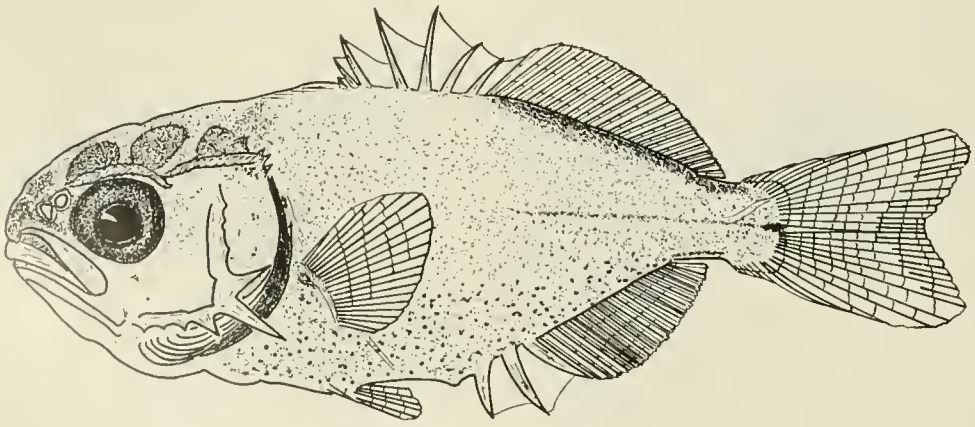

FIGURE 5.—*T. carolinus*, 11.0 mm. (*Gill* cruise 8, regular station 47).

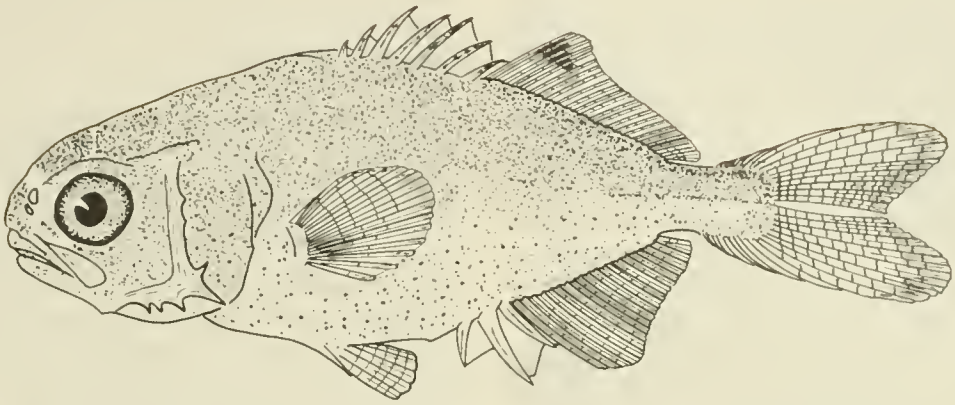

FIGURE 6.—*T. carolinus*, 14.8 mm. (East Beach, St. Simons Island, Ga.).

FIGURE 7.—*T. carolinus*. Upper, 18.9 mm. (King and Prince Beach, St. Simons Island, Ga.). Middle, 27.2 mm. (East Beach, St. Simons Island, Ga.). Lower, 42.1 mm. (King and Prince Beach, St. Simons Island, Ga.).

Florida in April and May. Full of nearly ripe spawn in April on the coast of Florida. . . ." Billy Christisen, an employee of one of the fish companies in Melbourne, Fla., on the Indian River, informed me (personal conversation) that over the years he has dressed hundreds of "pompano" (*T. carolinus*) and has never found any developed roe.

Springer and Pirson (1958: p. 177) speculated on the breeding season on the Texas coast—

> Pompano are caught all year long, but major catches occur during March, April, and May. These months are probably just prior to the breeding period as Gunter (1945) reports young as small as 13 mm. from June, and states that fish as small as 23 mm. were taken from June through December.

Nichols (1934: p. 46), referring to the lack of certain carangids (including *T. carolinus* and *T. falcatus*) in the Bermuda fauna, stated that—

> The probable explanation is that there are spawning grounds for these species in southern latitudes in or near the left (continental) edge of the Gulf Stream, and none on the opposite side.

The collection of two small specimens of this species in offshore waters indicates that *T. carolinus* spawns in the open ocean, either in the Gulf Stream or in locations where the transport and distribution of the eggs and larvae are influenced by this current. Two small specimens collected in offshore waters, were examined in this study. The first, 7.2 mm. (fig. 4), was taken near the 100-fathom line on *Gill* cruise 3, regular station 42 (31°57′ N., 79°16′ W), August 5, 1953. The other, 11.0 mm. (fig. 5) was taken on *Gill* cruise 8, regular station 47 (32°40′ N., 79°00′ W), September 25, 1954.

Recruitment

Young *Trachinotus carolinus* first appear on the Georgia beaches during the last half of April or

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the first half of May. This recruitment consists of small specimens, 11–20 mm., with a few as large as 30 mm., but largely in a size range of 13–18 mm. This first wave is followed at about monthly intervals by similar waves until the fish leave the beaches in late October to early December. By the first half of July, three size modes are recognizable; the largest (in size) representing the first wave, the smallest representing the most recent recruitment. From then to the latter part of October two or three size modes are recognized.

The fish apparently leave the beaches at about 60–70 mm., because only an occasional straggler of that size or larger is taken by beach seining. Therefore, fish apparently from the first wave leave the beach in the latter half of July, followed by the second wave in August, et cetera.

Analysis of seine collections of the Biological Laboratory at Brunswick, Ga., for the years 1956, 1957, and 1959 indicated that initial recruitment may represent the major spawning because the numbers of individuals collected during April and May for each year comprise about 56–66 percent of the total number of individuals taken in each year.

Recruitment continues into late October to early December, at which time 13.6- to about 50-mm. specimens are found on the beach, with an occasional larger straggler.

Water temperatures follow a consistent annual cycle on the open beaches in the Brunswick, Ga., area, especially during the warmer months. For the years 1956–59, the average monthly water temperatures (° C.), based on biweekly records from King and Prince and East Beaches, were for April, 21°; May, 26.6°; June, 27.8°; July, 30.5°; August, 30.3°; September, 28.6°; October, 24.2°; and November, 19.0°. The highest temperature recorded for this period is 33.0°.

Salinity of the beach water during the period 1956–59 was very erratic, with variations as high as 8.39 parts per thousand occurring in the same month and with 17.07 p.p.t. and 36.65 p.p.t. the extreme readings for April through November.

Based on the data for the years 1956–59, *T. carolinus* first appears on the Georgia beaches when the water temperature rises to about 19° C., leaves in the fall when the water cools to about the same temperature, and has been taken at both salinity extremes (17.07–36.65 p.p.t.).

Gunter (1945: p. 59) stated that *T. carolinus* was taken on the Texas gulf beaches in a temperature range of 19.0° to 30.7° C., and a salinity range of 28.1 to 36.7 p.p.t.

Size

Examination of seine collection data reveals little as to the growth rate of these fish. It is impossible to tell if consecutive collections were made from the same local population of a recruitment wave or from migrants along the shore. Another factor affecting growth analysis is the possible sporadic immigration to and emigration from the beaches of individuals comprising the wave; i.e., when the initial portion of a wave is sampled as it first reaches the beach, many individuals, especially of the smaller sizes, may not as yet have arrived. The same may be true in reverse at large sizes when the fish begin to leave the beaches. Probably the larger individuals in a wave move out first, and the emigration is possibly a random movement. Efforts to establish growth rates from existing samples produced little other than an indication that the growth rate of these young fish is probably 14–30 mm. per month, averaging about 22 mm.

Maximum size of *T. carolinus* was not resolved. Evermann and Marsh (1902: p. 140) stated that *T. carolinus* "reaches a maximum length of nearly 2 feet and a weight of 6 or 8 pounds." According to Hildebrand and Schroeder (1928: p. 231), "This pompano reaches a weight of about 5 pounds." Gregg (1902: p. 55) stated—

> The market fishermen of Indian River and Lake Worth *do* think the "true" or Common Pompano have been caught weighing up to 27 pounds. I have often been told of specimens weighing 20 to 25 pounds. I am quite sure the one caught by Capt. Gardner at Lake Worth April 15, 1898, was a true Pompano, as he was compared with several undoubted Pompanos . . . .

Present-day market fishermen on the Indian River confirm Gregg's observations. Some of these fishermen, who are well acquainted with *T. carolinus*, assert that they have seen fish in the 30-pound class that they identify as large "pompano." The Indian River fishermen differentiate between *T. carolinus* and *T. falcatus* by the colloquial name "pompano" for the former and "permit" for the latter. *T. glaucus* is unknown to them as an inhabitant of Indian River.

Food

The food habits of *T. carolinus* are well known. Goode (1882: p. 38) stated that "their food con-

sists of mullusks, the softer kinds of crustaceans, and probably, the young of other fishes." According to Evermann and Marsh (1902: p. 140), "The food of this fish seems to consist very largely of small bivalve shells and small crustaceans." Tracy (1910: p. 113) listed "Stomach contents: fishes, small crustacea, amphipods, lamellibranch shells, diatoms, and vegetable debris. Often seen rooting or digging in the sand for food . . . ." Gunter (1958: p. 189), referring to *T. carolinus*, stated "The little pompano feed to a large extent on young *Harengula*, and are commonly found in the summer with their stomachs distended with them." Stomach contents of *T. carolinus*, 13.5–80.5 mm. from the Georgia beaches, were found to contain amphipods, bivalve mollusks, crab larvae, copepods, isopods, and invertebrate eggs, in that order. Also found were small sessile barnacles, polychaetes, cumacea, unidentified small crustacea, and other invertebrates. Sand was quite commonly found in the stomachs, confirming Tracy's observations. Indian River market fishermen state that it is not uncommon to see several "pompano" accompanying large rays, particularly the spotted eagle ray, as they feed, supposedly feeding on mollusks and crustacea uncovered by the rays and also on morsels the rays fail to ingest.

Color

Meek and Hildebrand (1925: p. 385) stated that the color of *T. carolinus* is "bluish above, silvery below; ventrals pale; other fins usually black or dusky." Smith (1907: p. 214) gave the color as "bluish or greenish on back, silvery on sides, rich golden yellow below; fins with bluish or yellowish shades." Ginsburg (1952: p. 80) stated that coloration is "Silvery, with a grayish tinge on upper half, lighter below; fins dusky in the larger specimens, usually almost uniformly so; no cross bands." Bean (1903: p. 444) gave the color as "Uniform bluish above, sides silvery, golden in the adult, without bands, fins plain silvery or dusky."

Beach specimens (20–40 mm.) freshly killed in formalin exhibited the following coloration:

Chin, branchiostegal region, and ventral surface of body anterior to pelvic base white. Belly and lower sides of body from pectorals to caudal base silvery-white flecked with plumbeous chromatophores. Dorsal surface and upper sides of head and body metallic blue-green. Spinous dorsal with hyaline interspinous membranes; spines dusky, especially along leading edges. Anterior part of soft dorsal virtually black, because of the concentration of melanophores between first six or seven soft-rays. The lobe is dusky to the tip. Remainder of soft dorsal hyaline along its distal margin and proximal third of fin; base and area between hyaline parts lightly dusky. Interspinous membranes and basal portion of soft anal fin hyaline; spines, leading edge of soft anal, lobe, and distal margin distinctly yellow. Scattered melanophores form dusky lines between first three or four pectoral soft-rays; rest of pectoral fin yellow along proximal half and hyaline toward tip. Pelvic fins bright yellow-white. Lobes of caudal fin bright yellow, flecked with melanophores, causing outer principal rays to appear dusky. Coloration diminishes toward inner rays. Upper secondary caudal rays dusky and lower ones hyaline. Eye with black pupil and silvery iris with lightly dusky patch above and below the pupil.

Live *T. carolinus* kept in aquariums exhibited limited ability to change color. Small specimens (15–30 mm.) were able to change body pigmentation from silvery to very dusky, with an intermediate "peppered" stage. Individuals above about 30 mm. constantly maintained a uniform silvery body color. Generally, live specimens in the 30–50-mm. range showed very little duskiness on the body and fins, except for the leading edge and lobe of the dorsal fin, which is opposed to the duskiness on the fins and bodies of preserved specimens (fig. 7).

Parasites

Linton (1905: p. 330–335, 366) listed the following organisms found to be parasitic on *T. carolinus:*

Protozoa: *Myxobolis* (*Henneguya*) sp.; Nematoda: Immature nematodes (*Ascaris*) usually encysted in viscera. Cestoda: *Rhynchobothrium* sp. (encysted) in mesentary and on viscera; *Scolex polymorphus* Rudolphi. Trematoda: *Aspidogaster ringens* Linton; *Distomum monticellii* Linton; *Distomum pectinatum* Linton; *Distomum valde-inflatum* Stossich; *Distomum vitellosum* Linton; *Distomum* sp.; and *Monostomum* sp.

The soft fins of small specimens of *Trachinotus* spp. are often deformed or atrophied by cysts that adhere to the rays. Mild infestations seem to cause little damage, but concentrated infestations

destroy parts of the rays and other parts of the fins.

Status of *Trachinotus argenteus*

Ginsburg (1952: p. 82) considered *Trachinotus argenteus* Cuvier synonymous with *T. carolinus*, and I agree.

The original description, translated by DeKay (1842: p. 116), is as follows:

The Silvery Trachinote

Trachinotus argenteus

Characteristics. Silvery. Height to its length as one to two. 5–6 dorsal spines, and one recumbent, directed forwards. Length six inches.

Description. Body elevated; its height being one-half the head and body alone, without including the lobes of the tail, which are more than one-fourth the total length. Lateral line irregular, with five or six slight undulations. Five and sometimes six free spines on the back, without including the recumbent spine in front, nor that which adheres to the dorsal. The rays of the dorsal and anal exceed in number most of their congeners. The points of the dorsal and anal, when lying supine, reach only half the length of these fins. The limb of the preopercle with slightly elevated radiating lines, and oblique striae on the base of the opercle. Teeth minute, equal and velvet-like. Vertebrae compressed, twenty-three. The recumbent spine is a part of the third interspinous.

Color. Silvery, with blackish at the elongated tips of the dorsal, and on the middle of the pectoral.

Length, 6.0.

Fin rays, D.5 or 6 . 1 . 24; P . 18; V. 1 . 5; A . 2 . 1 . 21; C . 17 8/8.

Jordan (1887: p. 531), referring to the type, stated that "It may stand as *Trachinotus carolinus.*"

Various authors differentiate between *T. carolinus* and *T. argenteus* on the basis of depth, with *T. argenteus* having a depth of 2 into standard length and *T. carolinus* a depth of about 2⅓ to 2⅔ into standard length. Bean (1903: p. 443) stated—

There is still some question whether or not the *argenteus* of Cuvier and Valenciennes is the young of *T. carolinus* (Linnaeus). If we consider them identical we must assume that the very young, say from 1 inch to 2 inches long, are much more elongate than when they reach the length of 3 inches.

Ginsburg (1952: p. 81, table XV; p. 82) has shown that *T. carolinus* with depths greater than 50% S.L. are found in a size range of about 66–274 mm. My findings coincide with his except that my depth percentages are slightly less. This is no doubt because of a difference in method of measurement. One 182-mm. specimen examined in this study has a depth 55% S.L. It is identical to the typical *T. carolinus* in every respect but depth.

TRACHINOTUS FALCATUS (LINNAEUS)

Trachinotus falcatus, the round pompano (figs. 8–13), is a widely distributed and fairly common species. The Florida fishery produced a total of 98,503 pounds of "permit," presumably this species, during 1955–58, valued at about $10,288 (Anderson and Power, 1957; Bureau of Commercial Fisheries, 1959; Power, 1958 and 1959).

Knowledge of the life history of *T. falcatus* is meager. Since the species is generally not so plentiful nor as commercially important as *T. carolinus*, it seemingly has failed to attract comparable attention.

Spawning

Four offshore specimens identified as this species were taken during the operations of the

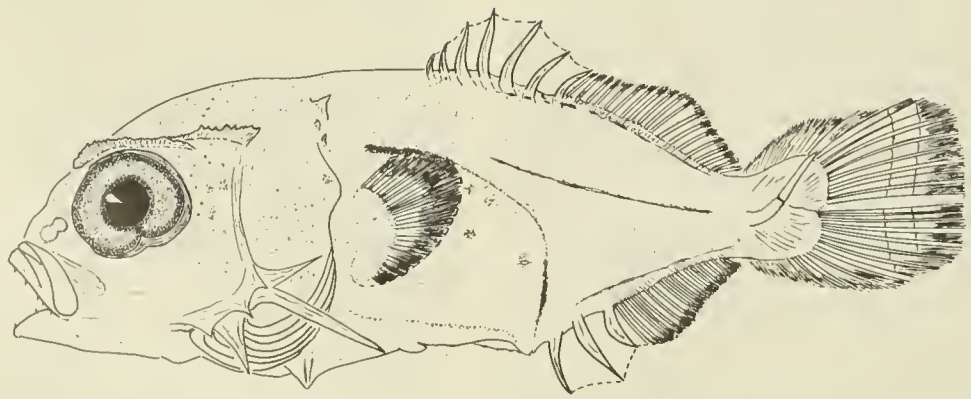

FIGURE 8.—*T. falcatus*, 5.0 mm. (*Gill* cruise 3, regular station 63).

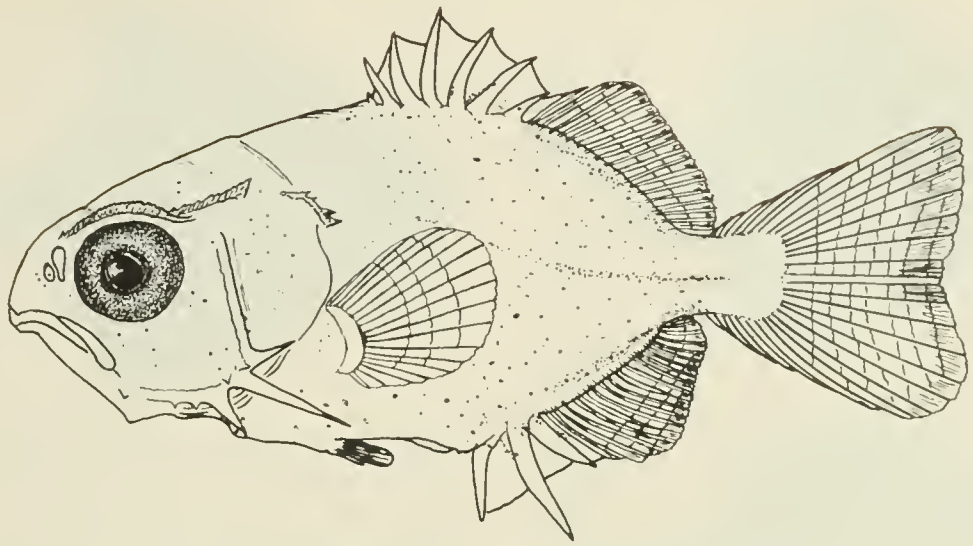

FIGURE 9.—*T. falcatus*, 7.7 mm. (*Gill* cruise 2, regular station 40).

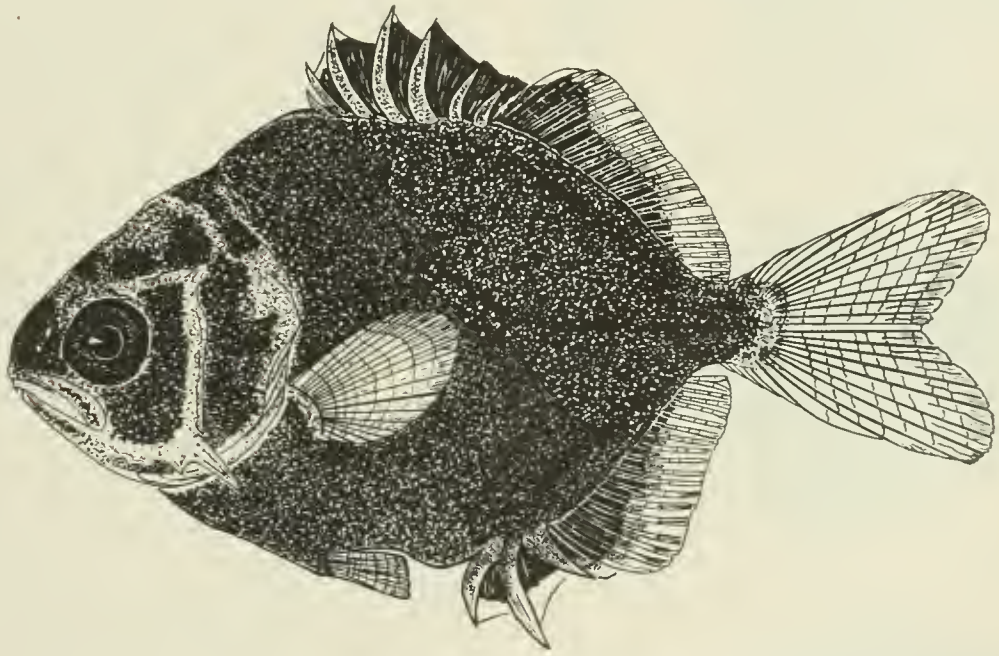

FIGURE 10.—*T. falcatus*, 16.9 mm. (King and Prince Beach, St. Simons Island, Ga.).

Gill (figs. 8 and 9), of which three were taken in close proximity to the axis of the Gulf Stream and one was taken at about the 100-fathom line. A fifth specimen (11.7 mm.), dip-netted aboard the M/V *Delaware*, was taken at 37°30′ N., 68°10′ W., about 360 miles east of Cape Charles, Va. The location of capture of these fish indicates offshore spawning habits for the species, in close proximity to or in the Gulf Stream.

Recruitment

T. falcatus arrives on Georgia beaches in late May or early June at a size range of 18 to 44 mm. From shortly after initial beach recruitment until the end of August it is never as abundant as *T. carolinus*, nor is there any apparent "wave." The beach population consists of scattered 14- to 66-mm. individuals. Between the first of September to the middle of October a major influx of

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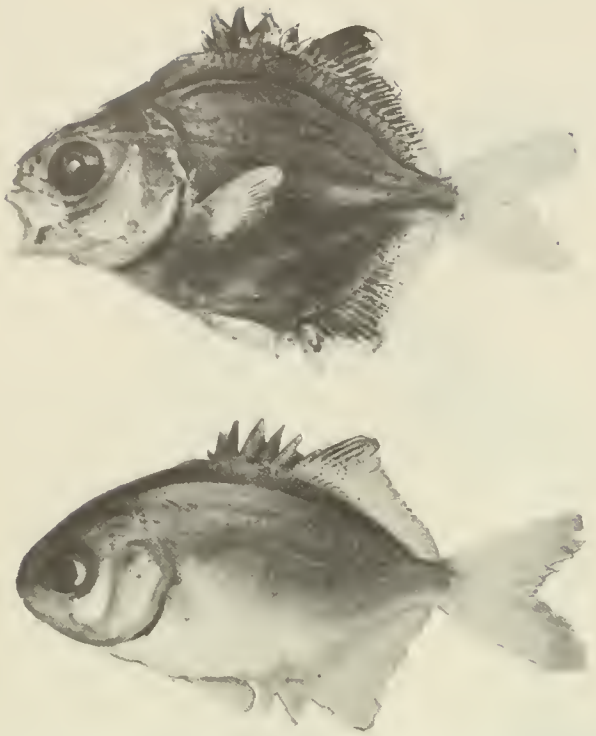

FIGURE 11.—*T. falcatus.* Upper, 23.6 mm. (Capers Inlet, S.C., ChM 31.207.12). Lower, 26.2 mm. (Fort Pierce, Fla., Phillips collection).

FIGURE 12.—*T. falcatus.* Upper, 35.3 mm. (Capers Inlet, S.C., ChM 31.207.12). Lower, 35.5 mm. (Fort Pierce, Fla., Phillips collection).

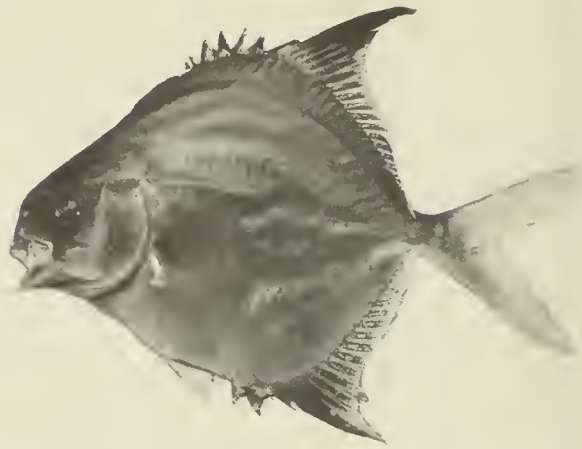

FIGURE 13.—*T. falcatus.* 59.5 mm. (Little River, 1 mile northeast of Calabash, N.C.).

small, 12- to 40-mm. fish appears on the beaches, supplementing the scattered population of larger fish. One to three size modes may be present at this time. Its stay is very short, for by latter October only a few individuals remain, these in the 14- to 65-mm. size range, and none is found after the middle of November.

Examination of material from southern Florida reveals a much different recruitment pattern than that found on the Georgia coast (See Phillips Collection, appendix table 1). In the Miami-Vero Beach area, specimens were taken throughout the year and generally at much smaller sizes than in Georgia. Specimens less than 12 mm. long were taken from January into September. The nearness of the Gulf Stream to the southern Florida coast no doubt influences the long period of beach recruitment and the small size of the inshore specimens. This pattern indicates a prolonged spawning season, much of which is restricted to subtropical waters.

Based on water temperature and salinity data for the years 1956–59 (see under *T. carolinus*, p. 194), *T. falcatus* first appears on Georgia beaches when the water is warmed to about 27° C., and remains on the beaches until the water cools to about 19.5°, and has been taken in a salinity range of 17.07–35.34 parts per thousand.

Size

Beebe and Tee-Van (1928: p. 116) stated that *T. falcatus* "Grows to 12 inches and a weight of 3 pounds." Breder (1948: p. 139) said that it reaches a length of about 18 inches. Ginsburg (1952) examined a specimen 790 mm. (about 31

in.) long. The maximum size attained by this species was not determined.

Food

Stomachs of Georgia beach specimens (15.1–53 mm.) contained isopods, amphipods, sessile barnacles, calanoid copepods, crab larvae, bivalve mollusks, flatworms, stomatopods, unidentified crustacea, and diptera (pupae and adults).

Form and Color

Marked variations in form and color of small *T. falcatus* have been noted by various authors. Mrs. Craig Phillips (personal communication) observed—

> The several dozen specimens I have seen . . . from the St. Simons (Georgia) area differ in several respects from the form most common in south Florida . . . The fish (from St. Simons) are almost invariably dark, reddish brown when netted. They are quite robust with an impressive depth, and dorsal and ventral profiles that are quite angular. This form is present south at least as far as the upper Keys. However the form that I have found to be most common from Ft. Pierce (Florida) southward is invariably silver when netted except . . . individuals less about 20 mm., and these become gradually darker in pigment as their size decreases. This form appears to be more slender with less angular dorsal and anal profiles. . . .

Breder made the following observations regarding *T. falcatus*:

> Three examples about 24 mm. in standard length . . . were a smooth velvety black and the fins were hyaline. Two of these were kept in the Aquarium for a few weeks and lost this pigmentation becoming a silvery color similar to the young of *T. carolinus*. The iris in life was a deep ruby red (1923: p.3).
>
> A single example of 24 mm. was taken. . . . Body reddish black with silvery reflections. Iris silver. Dorsal and anal spines red, membranes of soft dorsal and anal dusky. Pectorals and ventrals hyaline, the latter edged anteriorly with deep orange (1926: p. 125).
>
> These were about 20 to 30 mm. in length (without tail) and were passing out of the dark phase. The red of the iris was completely gone and the coloration was nearly as silvery as that of *T. carolinus*, with just a faint dusky suggestion (1928: p. 6–7).

Beebe and Tee-Van (1928: p. 116) noted that—

> Great variation exists among the small specimens taken in Haiti, and the variations change while the fish is being watched. Some of these small fishes instead of being silvery, have parts of the sides a warm brown, usually unsymmetrically. Descriptions from life . . . are given below:
>
> 13 mm. Entire body thickly covered with small brown spots, so close together that the paler ground color is almost obliterated; the brown color absent on the maxillary premaxillary and on the branchiostegal membranes. Top of head brick-red. Membrane of the spinous dorsal and base of the anterior membranes of the soft dorsal black, the black on the soft dorsal becoming less as it progresses backward. A few black dots on the dorsal spines. Base of the anal, membranes between the anal spines and the anterior membranes of the anal fin black. All other fins pale.
>
> 15 mm. Two specimens of this length were recorded as being iridescent bronze throughout; the iris and thickened web about the dorsal and anal spines grenadine red; the web between these spines and the basal half of the dorsal and anal rays black.
>
> 45 mm. Bluish silvery, with minute blackish punctulations over the entire body with the exception of the lower chin, isthmus and just before the ventrals. Dorsal membranes dusky. Anal membranes dusky basally, the duskiness decreasing posteriorly. Pectorals clear. Tips of the ventrals, the anal spines and tip of the anal lobe orange-red.

Gunter (1958: p. 190) was seemingly confused by the color variation. He stated—

> Another species, at a size of 23 mm., was dusky or blackish, had reddish orange dorsal spines and a reddish orange eye. It seemed to be *T. falcatus*. . . . A third species, at a size of 23 mm., was reddish orange on the lower caudal lobe, the anal fin edge and large spine. It was called *T. goodei*, which Ginsburg synonymizes with *T. glaucus*, and probably belonged to the latter species.

Color notes of live and preserved specimens, made during my study, corroborate these observations. A 9.8-mm. specimen (preserved) from Fort Pierce, Fla., has the following color characters:

Body above midline and behind pectoral base brown. Large deep melanophores on sides of abdomen. Area behind abdomen and below midline with small scattered brown chromatophores and melanophores on flesh-colored background. Large deep melanophores and brown chromatophores along dorsal base, anal base and posterior part of midline, extending onto caudal peduncle, giving the effect of dim lines running along these areas. Spinous dorsal and spinous anal area dark brown. Other fins hyaline.

Three specimens (59–61 mm.) had these color characters when fresh:

Chin, isthmus, gill covers, area below eye and body below lateral line silvery-white (on one fish, light orange on a white background shows on lower limb of preopercle, mandibular articulation, chest and anal region). Body above lateral line and dorsal half of head light metallic. Dorsal spines and membranes between spines plumbeous; soft dorsal dusky, especially on lobe. Anal spines

and soft-fin lobe very bright orange; outer margin of soft anal hyaline, remainder dusky. Pectorals dusky at base, hyaline elsewhere. Pelvics with white background interspersed with very bright orange. Caudal with orange-yellow on most of lobes; outer rays dusky almost to tips; inner rays grading to hyaline. One 39.5-mm. specimen had much the same coloration except that it was duskier and the orange was more intense. My notes on a 64-mm. fresh specimen indicate similar coloration and give eye color as "pupil blue-black; iris coppery."

A single specimen, 17.6 mm., was kept in an aquarium and observed over a period of time. The following notes pertain to this specimen:

(1) June 5, 1958, at 1130 hours. Body silvery with slightly pinkish tinge on dorsal aspect. Spinous dorsal and soft fin lobe black; remainder with melanophores forming dusky lines between rays and along base. Spinous anal and soft fin lobe orange-red; remainder hyaline. Pectorals, pelvics, and caudal hyaline. Eye with pink-orange iris. At 1144 hours, body and fin color remained much the same, but iris was silvery.

(2) Undated, but between June 5 and June 9, 1958. Fish in aquarium—color as described June 5, 1958 at 1130 hours. Fish removed from aquarium and placed in beaker (of sea water); agitated by microscope light, and confinement. Posterior half of body turned dusky gray. Fish carried (outdoors) into direct sunlight—turned silvery. Returned indoors. Posterior half turned brown, then brownish color migrated to behind pectorals. When color began receding rearward, fish was agitated. Brown pigment covered entire body and head. Insertion of black or white background (into beaker) seemed to cause little immediate change in coloration. However, when left against white background for about 20 minutes, the top of head and back in front of spinous dorsal became a blotched flesh color. Fish returned to aquarium. After about 10 minutes, the coloration was silvery, as first described.

Subsequent tests with the same fish yielded similar results. Usually when the fish was disturbed the posterior half of the body turned uniformly dark brown first and then the color migrated anteriorly. The intensity of color change and the time involved varied considerably. The fish also showed some color changes when undisturbed in the aquarium. Usually these changes involved duskiness or blackness on areas of the body and on the dorsal lobe.

Variations in body depth in *T. falcatus* are considerable and exhibit no distinct relation to geographical location or time of year. Generally, fish taken at the same time and location have comparable depths, but specimens taken at different times from the same location and from different locations have widely diverse depths. Figure 18 illustrates the depth differences, expressed as percent of standard length of fish taken at five locations along the south Atlantic coast. Two of these locations, King and Prince Beach, St. Simons Island, Ga., and Fort Pierce, Fla., are represented twice each.

Marked differences occur in coloration and dorsal and anal profiles in the depth extremes in *T. falcatus* (figs. 11 and 12), and a general correlation exists between these characters and depth; i.e., the deeper the fish, the darker the color and the more angular the profile. The shallow Fort Pierce specimens have silvery sides and very little pigmentation on the vertical fins. They are also definitely "popeyed," and have uniform dorsal and anal profiles. Deep-bodied specimens, such as the Capers Inlet, S.C. fish, have much dark pigmentation on the body and on the vertical fins. The eyes are "normal" and the dorsal profile is slightly concave on the head and strongly convex over the procumbent spines. Another break in dorsal profile sometimes occurs near the last dorsal spine. The ventral profile usually has a break at the third anal spine.

The greatest extreme in depth, color, and dorsal and anal profile was observed in a 59.5-mm. specimen from Little River, on the North Carolina–South Carolina border (fig. 13). As mentioned earlier, dark body coloration is usually restricted to smaller fish. This Little River fish, with a depth of 75.4% S.L., has a greatly accentuated profile, is very dark brown on the body, and possesses almost black vertical fins.

Beebe and Tee-Van (1928: p. 115) referring to *T. falcatus*, observed—

> Our fish differs from the photograph (Plate XXXIII) of a 48-mm. fish given by Meek and Hildebrand in that the depression over the eyes is not so marked. In all the specimens the profile from the nostrils to the dorsal fin is almost straight, with a slight convexity on the posterior part.

Meek and Hildebrand's (1925: Plate XXXIII,

facing p. 378) illustration of a 48-mm. *T. falcatus* obviously depicts a fish with abnormal development; i.e., clearly evident preopercular angle spines, very short dorsal and anal lobes, complete membrane connections between spines, and an exceptionally small caudal fin. The fish also has much dark coloration, and judging from the photograph the depth is about 73% S.L. This specimen and the fish from Little River may indicate a correlation between extreme body depth and abnormal rate of development.

Parasites

Linton (1940: p. 75–82, 156) listed the following organisms found to be parasitic on *T. falcatus*:

Trematoda: *Cymbephallus vitellosus* (Linton); *Cryptocotyle lingua* (Creplin) cysts on skin of body and fins.

TRACHINOTUS GLAUCUS (BLOCH)

Trachinotus glaucus, the palometa, (figs. 14–17), is comparatively rare along the south Atlantic coast. The main part of its range is farther

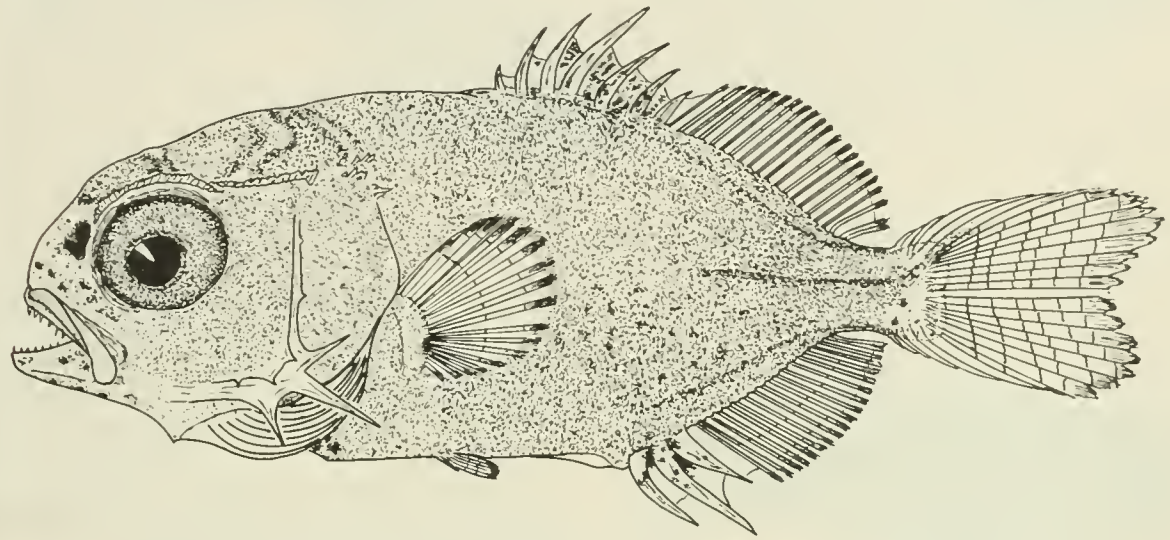

FIGURE 14.—*T. glaucus*, 7.8 mm. (Seaquarium boat dock, Miami, Fla., Phillips collection).

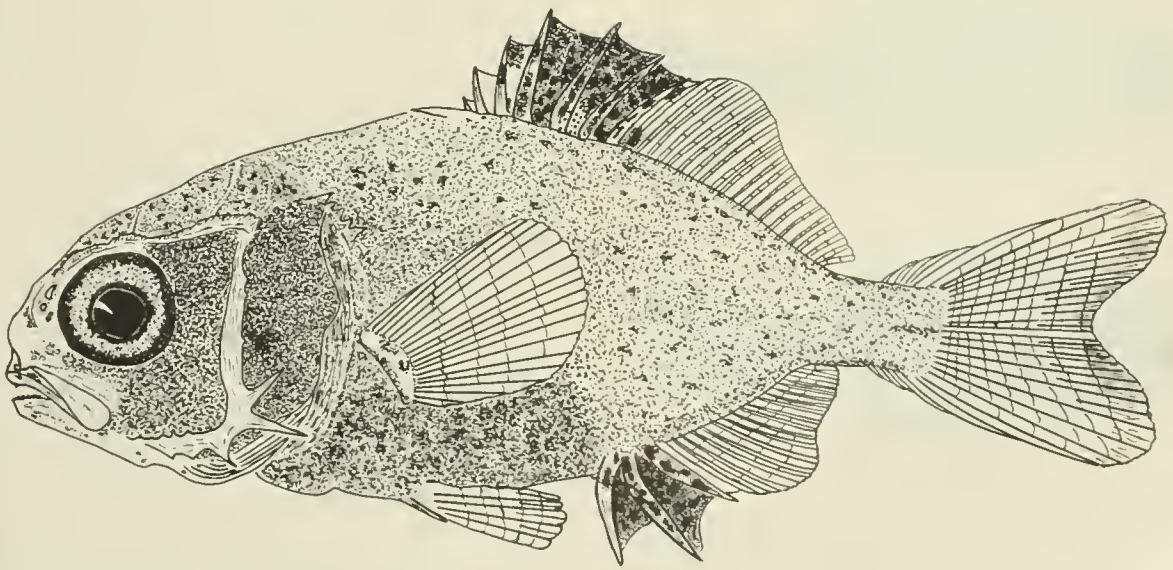

FIGURE 15.—*T. glaucus*, 11.8 mm. (Crandon Park, Miami, Fla. Phillips Collection).

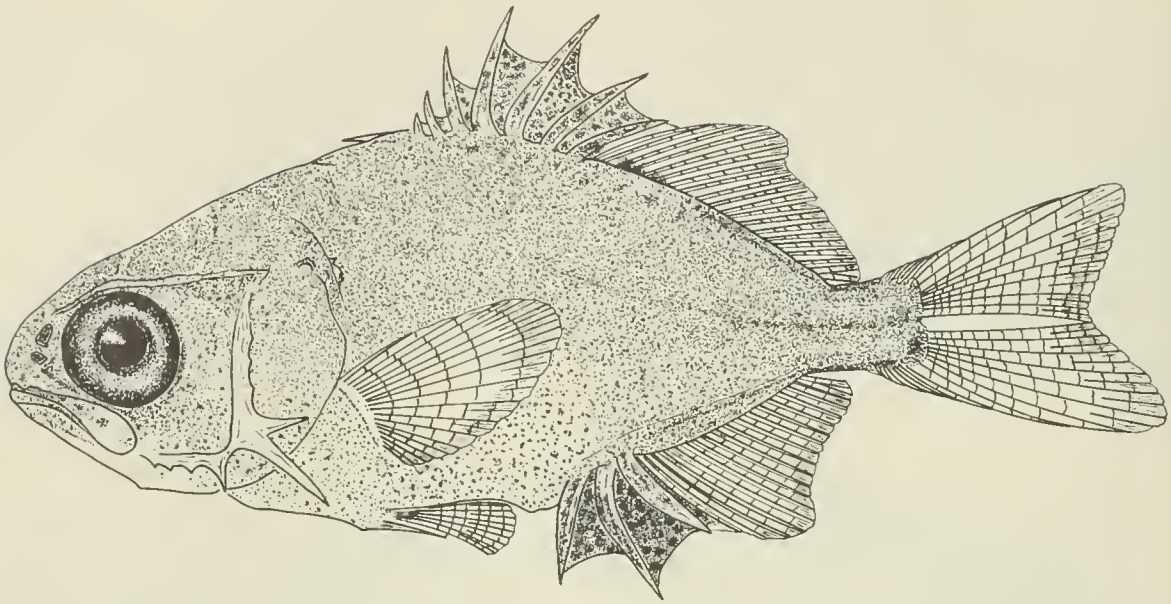

FIGURE 16.—*T. glaucus*, 14.6 mm. (Louisiana. USNM 143953).

FIGURE 17.—*T. glaucus*: Upper, 19.4 mm. (King and Prince Beach, St. Simons Island, Ga.) Middle, 28.9 mm. (King and Prince Beach, St. Simons Island, Ga.) Lower, 39.4 mm. (King and Prince Beach, St. Simons Island, Ga.).

south, and it is apparently not so abundant anywhere on the mainland as the other species.

Virtually nothing has been published about its life history, and the few individuals taken during the seining program of the Biological Laboratory at Brunswick on the Georgia beaches do little to augment present knowledge. Twelve individuals, 19.4–61.0 mm., have been taken. All were collected from August to November.

Size and Food

As with the other species, the maximum size of *T. glaucus* is uncertain. Beebe and Tee-Van (1933: p. 108) said that it grows to about a foot. Carvalho (1941: p. 55) stated that its food consists of crustaceans and small fish. Examination of stomachs of the Laboratory specimens produced amphipods, bivalve mollusks, diptera, stomatopods, hymenoptera, crabs, fish, and isopods, in that order of significance.

Color and Form

Evermann and Marsh (1902: p. 138) gave coloration as—

> . . . bluish above, golden below; lobes of dorsal and anal very dark; rest of fins pale, with bluish edges; caudal bluish; pectorals golden and bluish; ventrals whitish. Body crossed by four black vertical bands, . . . a black spot representing a fifth band on lateral line between last rays of dorsal and anal, ...

My specimens larger than 70 mm. exhibited very little color. The upper half of the body and

head was dull blue-gray, grading into white in the branchiostegal region, breast, lower sides, and belly. Dorsal and anal lobes black, remainder of these fins dusky. Pectorals slightly dusky; pelvics white. Caudal lobes very dusky along outer rays; lighter toward inner rays. Five dark vertical bars along sides of body.

Specimens 40 mm. and smaller can easily be confused with *T. carolinus* because of the similarity in coloration and depth of body. Fresh specimens exhibit dull silvery dorsal surfaces and light gray to white flanks and belly. The dorsal lobe is black; the anal lobe cinnamon and black (black in preserved specimens). The spinous dorsal and anal are pigmented. Other fins are very slightly dusky, except for the caudal, which is moderately dusky along upper and lower margins. There are no bars on the body of the laboratory specimens. Evermann and Marsh (1902: p. 138), referring to small *T. glaucus*, observed—

> Young individuals, 2 inches in total length, may be described as follows: . . . Color, bright-silvery, merging into metallic-bluish on back and yellowish on lower sides and belly; the four dark vertical bars very faint, but usually distinguishable with a lens, . . . anterior rays of dorsal and anal and outer rays of caudal black.

They also stated that—

> Comparing young examples in our collection from Porto Rico with specimens of similar size from Woods Hole which have been identified as the young of *T. goodei*, it is found that they are difficult to distinguish. The general form, proportional measurements, fins, and general coloration are very much alike, but the black vertical bars are apparently not present on the Woods Hole specimens.

Status of *Trachinotus goodei* and "Permit"

Ginsburg (1952: p. 76) placed *T. goodei* Jordan and Evermann in the synonymy of *T. glaucus*, an action my observations substantiate.

Trachinotus goodei Jordan and Evermann (1896: p. 943) is "described from a small specimen from Key West, the characters of the adult taken from Günther." Morphometric and numerable characters given in the description well fit a small *T. glaucus* of about 30–50 mm.: "Head 3; depth 2⅔. D. VI–I, 19; A. II–I, 17," and ventrals 2 in head; anterior soft-rays of dorsal and anal fins (dorsal and anal lobes) 4 in length of body, in the young; caudal lobes about 3 in body.

Examination of photographs of syntypes (Stanford University 1455) reveals specimens apparently identical to *T. glaucus*. Other specimens previously identified by other workers as *T. goodei* (USNM 68595 and 125672) are *T. glaucus*.

Ginsburg (1952: p. 72) aptly stated the basis of confusion related to *T. goodei* and the term "permit":

> The apparent existing misapprehension regarding the western Atlantic species of *Trachinotus* involves also a curious confusion of common and scientific names. In current accounts, the "permit" is generally treated under the name of *T. goodei*. However, as stated, the name "permit" apparently refers, partly or wholly, to large specimens of *falcatus*; while the type on which the name *goodei* is based, is evidently a small specimen of *glaucus* as noted under its account, and the name *goodei* must be entered in the synonymy of *glaucus*.

Further confusion results from the almost universal use of the term "permit" for any unusually large *Trachinotus*, and by its use for any *T. falcatus* on Indian River, Fla.

ONTOGENY OF *TRACHINOTUS* SPECIES

HEAD LENGTH

There is a gradual decrease in relative head length with an increase in standard length in the three species, *Trachinotus carolinus*, *T. falcatus*, and *T. glaucus*. Growth patterns in all species are essentially the same. Below about 10 mm., relative head length is about 39–44% S.L., and by about 200 mm. it has decreased to about 26–27% S.L. Above 230 mm., relative head length in *T. carolinus* is 25% S.L. or less (appendix table 2 and fig. 19).

Head lengths of 39.1% and 41.5% S.L. for the 3.07– and 4.0-mm. specimens (*Trachinotus* sp.) fall in line with the trend suggested by the data for the three species, but the value of 33.8% S.L. for the 4.66-mm. specimen is low (appendix table 2).

EYE DIAMETER

As in head length, there is a gradual decrease in relative eye diameter with an increase in standard length. Growth patterns in all three species are very similar, with *T. carolinus* and *T. glaucus* presenting virtually identical patterns and *T. falcatus* showing a slightly larger eye at any given length. Below 10 mm., eye diameters are about 13–16% S.L. for the three species, and by 210 mm. they are about 6–8% S.L. This relative decrease continues in *T. carolinus* and specimens above 300 mm. approach an eye diameter of about 5% S.L. (appendix table 2 and fig. 19).

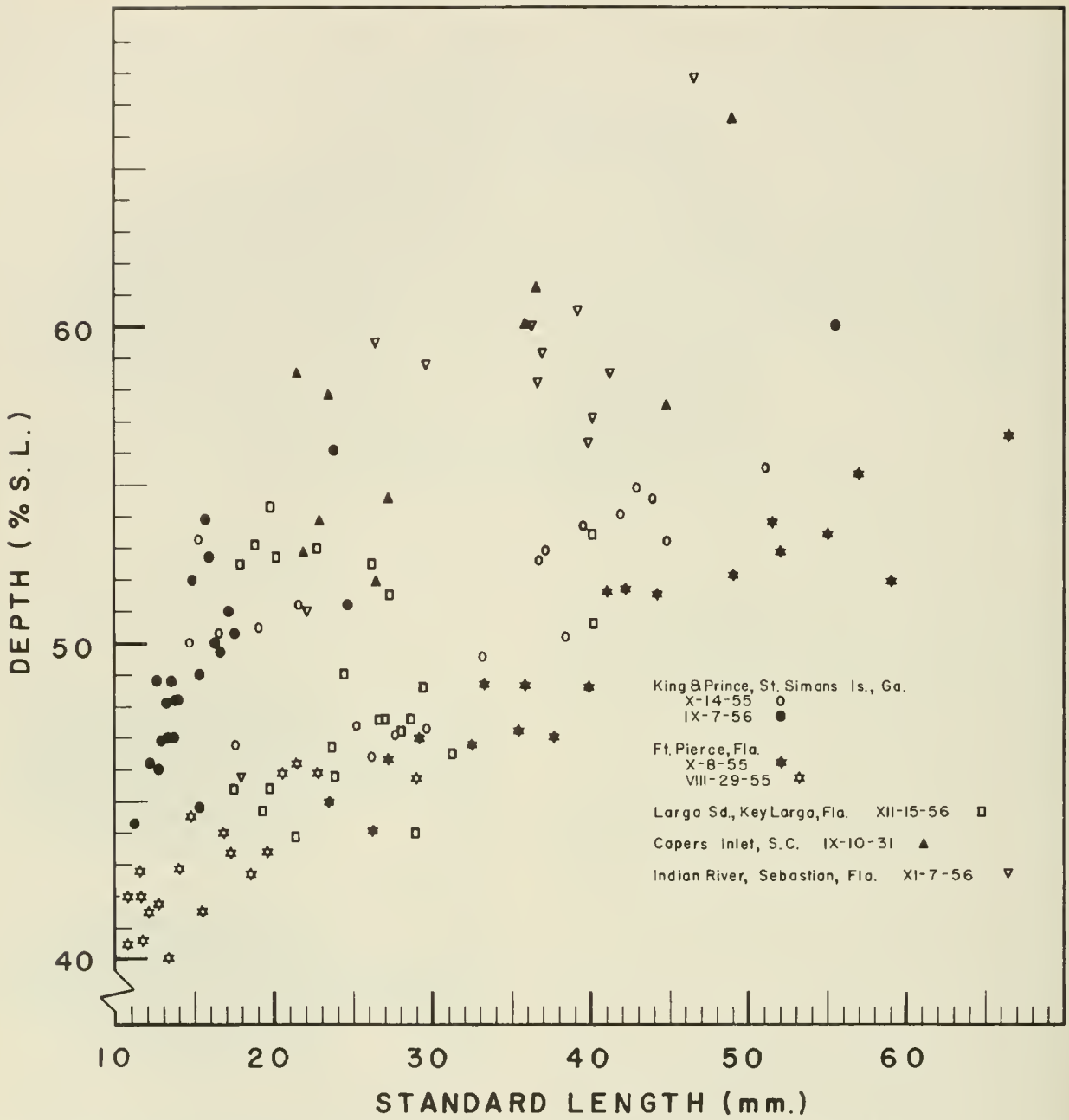

FIGURE 18.—Body-depth ranges for *T. falcatus*, expressed as percent of standard length. (Five sites on the south Atlantic coast of the United States and seven collecting dates are presented.)

In *Trachinotus* sp. eye diameters of the 3.07-, 4.0-, and 4.66-mm. specimens are 11.0, 13.2, and 11.2% S.L. (appendix table 2).

BODY DEPTH

Relative depth increases with an increase in standard length to about 120 mm. in all species. Growth patterns for *T. carolinus* and *T. glaucus* are similar, with *T. glaucus* slightly the shallower between 20 and 120 mm. *T. falcatus* is markedly deeper at all sizes. Below 10 mm., the relative depth for *T. carolinus* and *T. glaucus* is about 32–36% S.L. and increases to about 48–50% S.L. at 130 mm. Above 130 mm., this relative depth is maintained in *T. carolinus* to about 200 mm. after which it gradually decreases, with specimens about 300 mm. and above having a depth approaching 40% S.L. Below 10 mm., *T. falcatus*

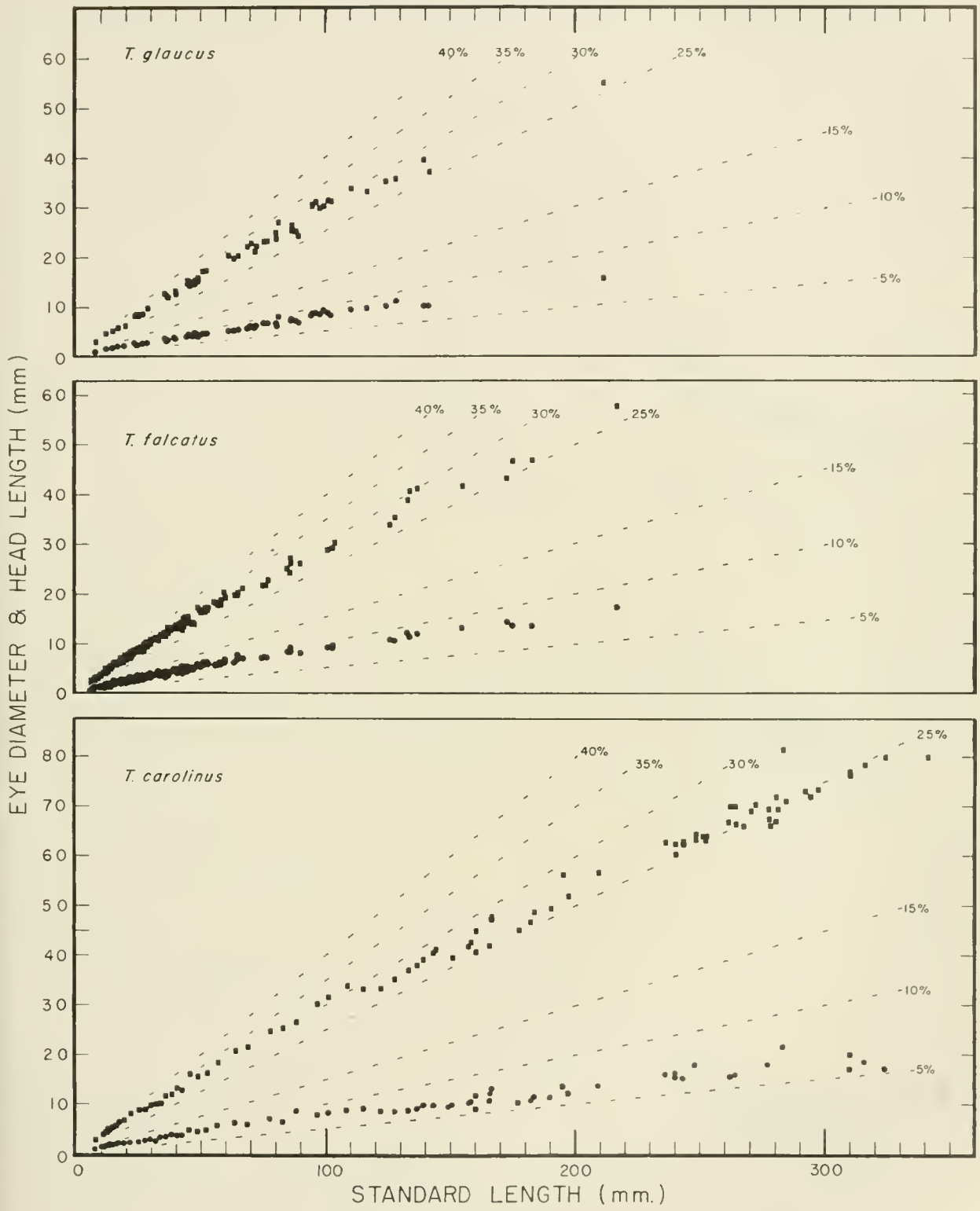

FIGURE 19.—Relation of head length (squares) and eye diameter (circles) to standard length for *T. carolinus*, *T. falcatus*, and *T. glaucus*. (Dashed lines and respective percentages are guides for determining the part dimension as percent of standard length.)

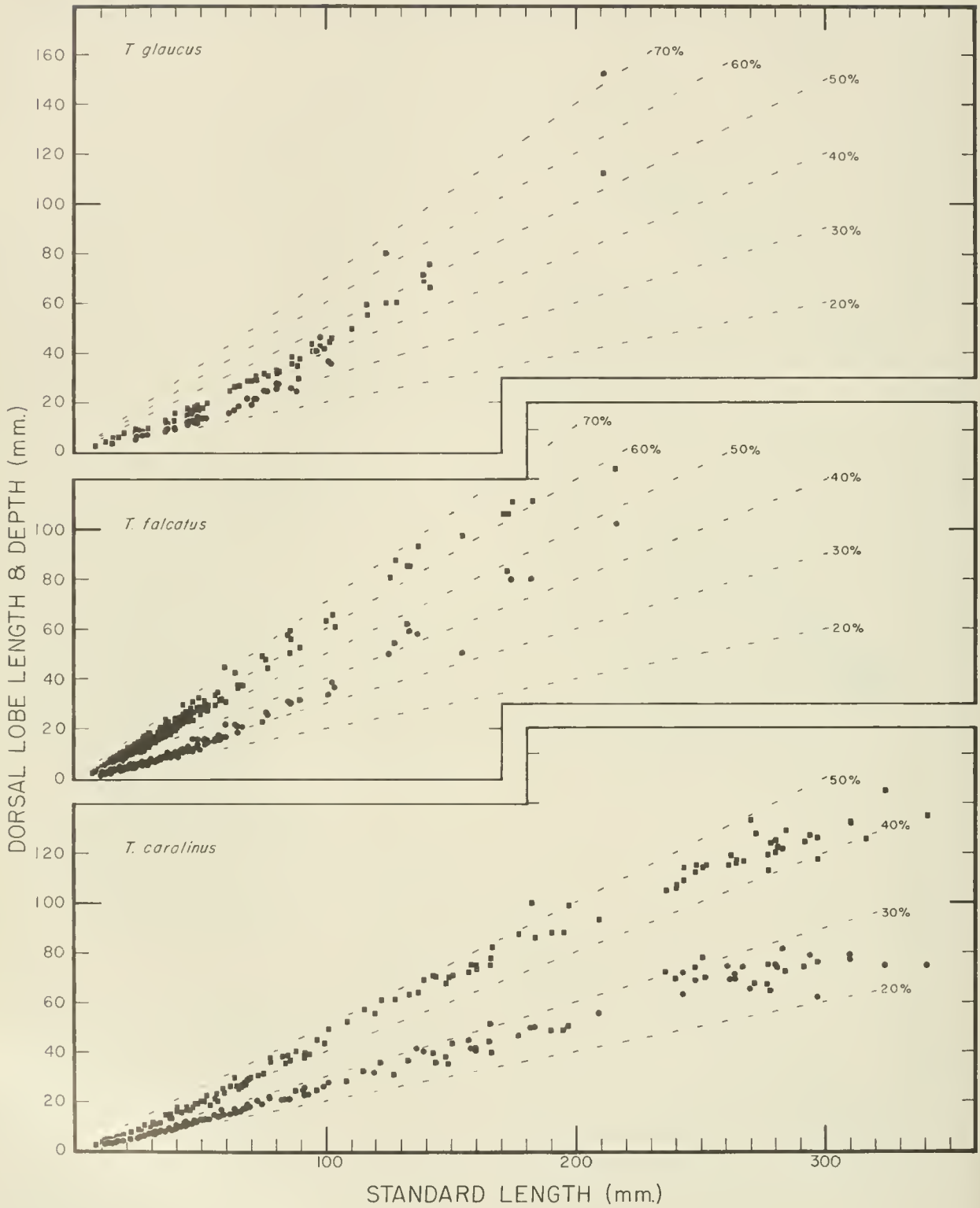

FIGURE 20.—Relation of body depth (squares) and dorsal-fin lobe length (circles) to standard length for *T. carolinus*, *T. falcatus*, and *T. glaucus*. (Dashed lines and respective percentages are guides for determining the part dimension as percent of standard length.)

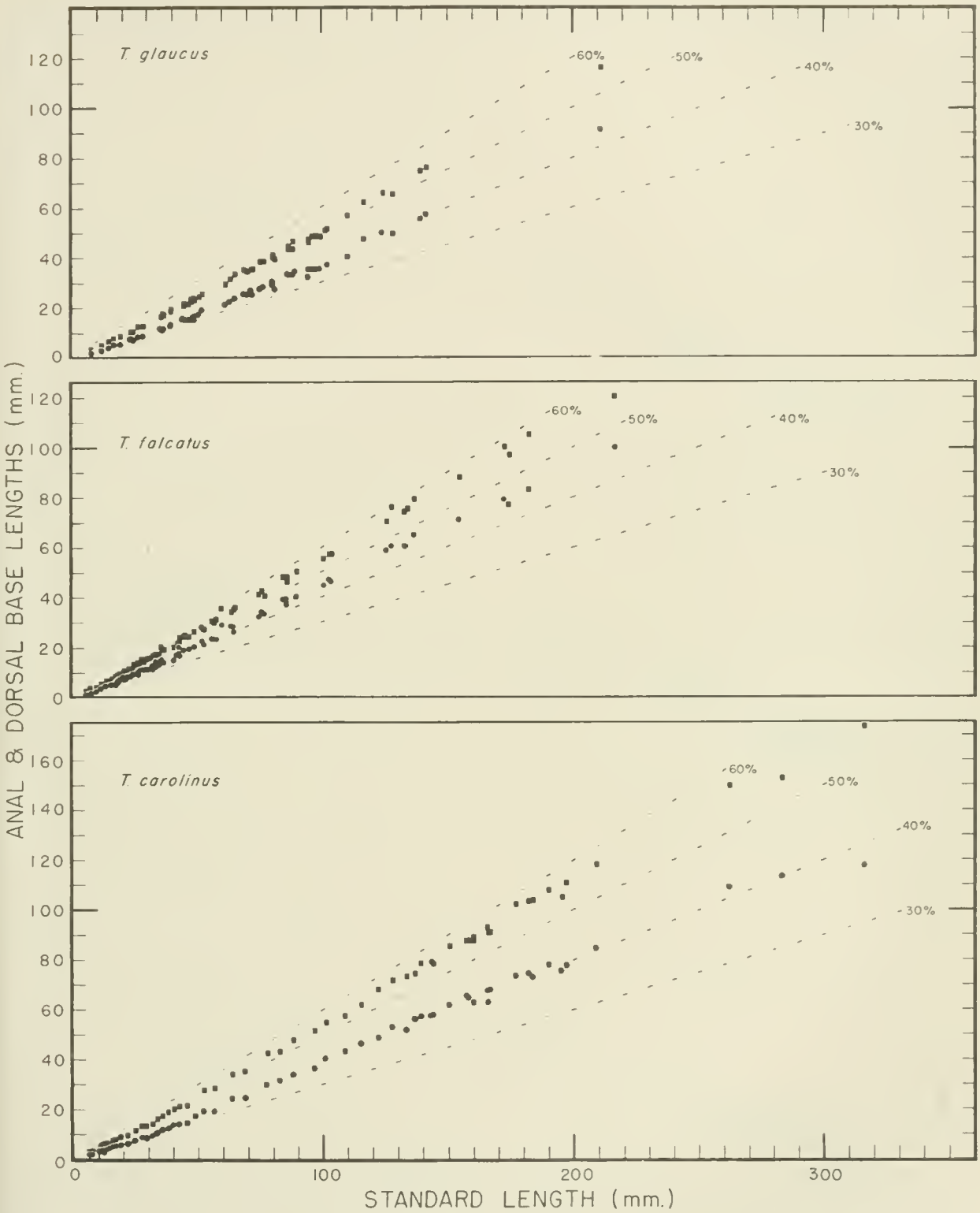

FIGURE 21.—Relation of dorsal-fin base length (squares) and anal-fin base length (circles) to standard length for *T. carolinus*, *T. falcatus*, and *T. glaucus*. (Dashed lines and respective percentages are guides for determining the part length as percent of standard length.)

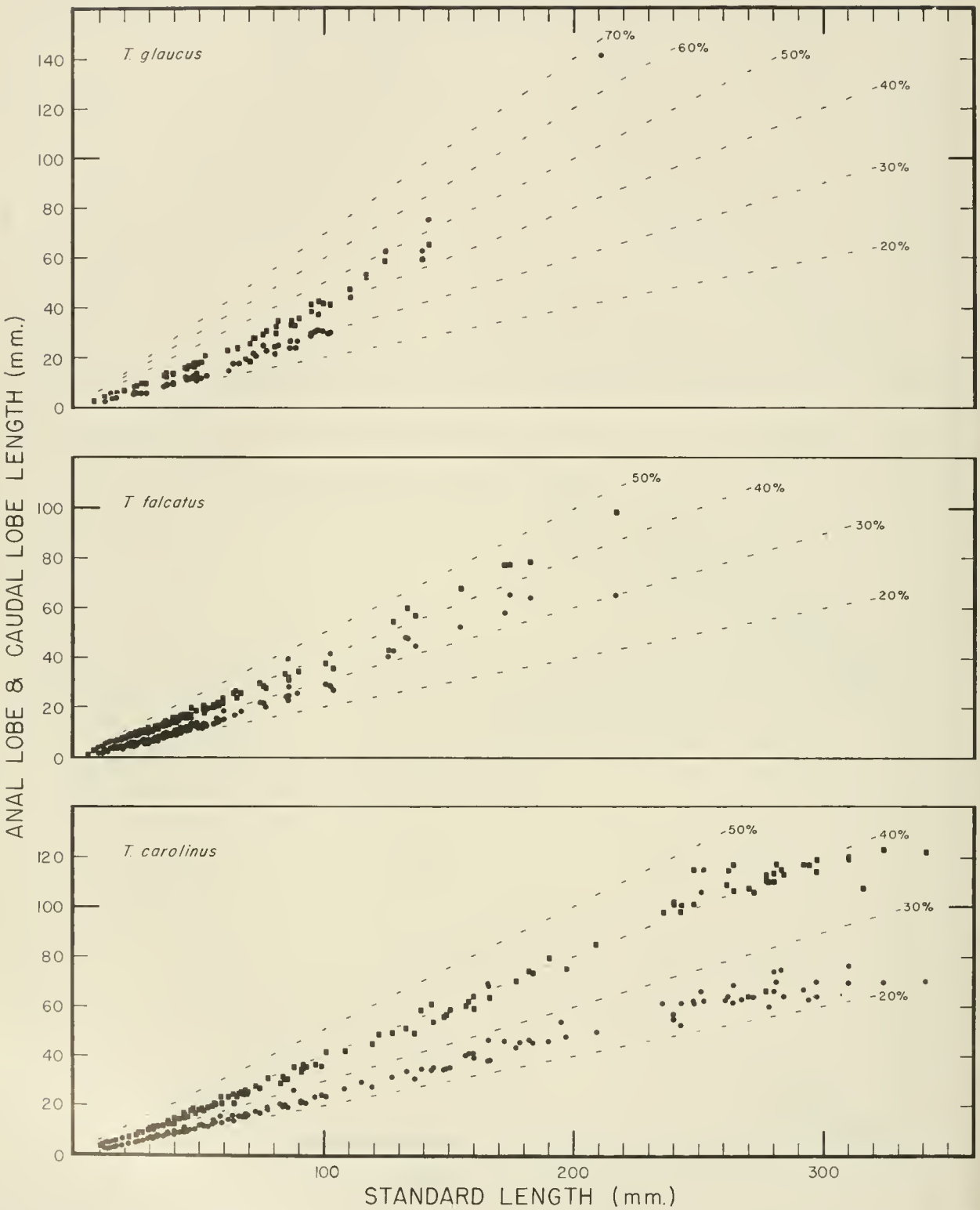

FIGURE 22.—Relation of caudal-fin lobe length (squares) and anal-fin lobe length (circles) to standard length for *T. carolinus, T. falcatus, and T. glaucus.* (Dashed lines and respective percentages are guides for determining the part length as percent of standard length.)

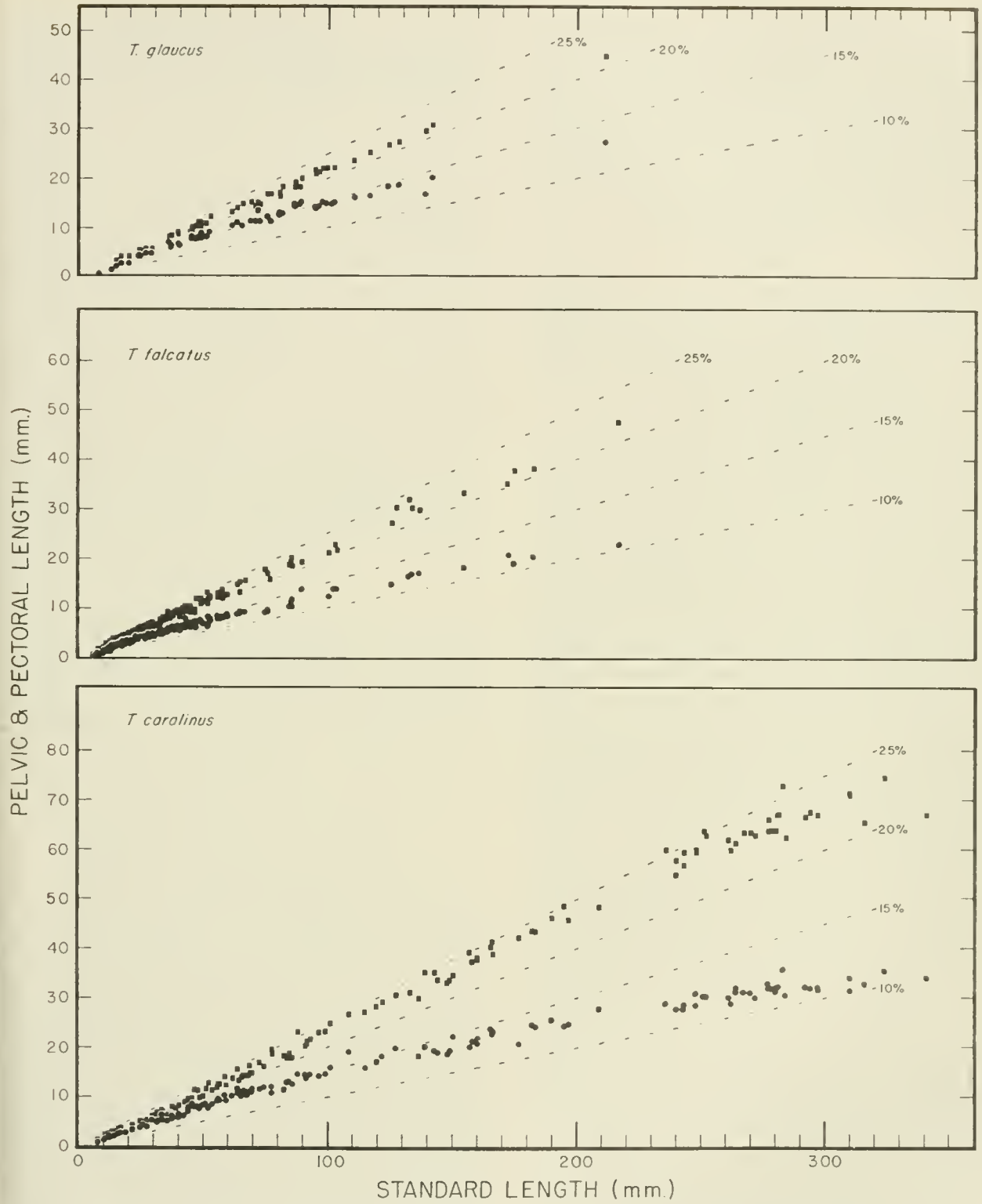

FIGURE 23.—Relation of pectoral length (squares) and pelvic length (circles) to standard length for *T. carolinus*, *T. falcatus*, and *T. glaucus*. (Dashed lines and respective percentages are guides for determining the part length as percent of standard length.)

has a relative depth of about 30–40% S.L. By 100 to 140 mm., depth has increased to about 60–68% S.L. Relative depth decreases at sizes above about 140 mm. and is less than 60% S.L. at about 200 mm. (appendix table 2 and fig. 20).

In *Trachinotus* sp., depths of the 3.07-, 4.0-, and 4.66-mm. specimens are 18.2, 19.2, and 20.2% S.L., respectively (appendix table 2).

DORSAL FIN

Elements

Trachinotus sp.—At 3.07 mm., no spines or soft-rays are discernible. At 4.0 mm., five spines and about seven soft-ray buds are barely discernible. At 4.66 mm., six spines and 20 soft-ray buds are present (figs. 1–3).

T. carolinus—Elements V to VI–I, 22 to 27. Ginsburg (1952) found that of 346 specimens he examined 51 had six (V–I) and 295 had seven (VI–I) spines; and that of 342 specimens examined 36 had 23 soft-rays, 183 had 24, 110 had 25, 12 had 26, and 1 had 27. Of 197 specimens examined in my study, 17 had six dorsal spines, and 180 had seven. Dorsal soft-ray counts were made on 172 specimens: One had 22, 12 had 23, 99 had 24, 55 had 25, and 5 had 26 dorsal soft-rays (table 1). Spines are prominent, and soft-rays are developed by about 7 mm. (fig. 4). At this size all but about six of the soft-rays are segmented; none is branched. All soft-rays are segmented by about 10 mm. Branching occurs at about 18–20 mm. in all soft-rays except the first (anteriormost), which branches at approximately 40 mm.

T. falcatus.—Elements VI–I, 17 to 21. Ginsburg (1952) examined 24 specimens and found all to have seven dorsal spines. One specimen had 18 dorsal soft-rays, 16 had 19, and 7 had 20. All 386 specimens examined for this character in my study had seven (VI–I) dorsal spines. One specimen had 17 soft-rays, 13 had 18, 255 had 19, 113 had 20, and 4 had 21 (table 2). Spines are prominent in the 5.0-mm. specimen (fig. 8), and the individual soft-rays discernible. No segmentation or branching has occurred. By about 6.5 to 9 mm. all but 1 to 3 soft-rays have segmented. All are segmented after about 9.5 mm. Branching begins at about 12 mm., and all soft-rays except the first are branched by about 17 mm. Branching is completed by about 20 to 24 mm.

TABLE 1.—*Dorsal and anal soft-ray relation for 172 specimens of* Trachinotus carolinus

[Upper numbers in blocks represent specimens with the indicated combination; numbers in parentheses represent approximate percentage of the sample with that combination]

ANAL SOFT-RAYS	DORSAL SOFT-RAYS 22	23	24	25	26	Total anal rays
20	1 (0.6)	2 (1.2)	5 (2.9)			8 (4.7)
21		9 (5.2)	40 (23.3)	13 (7.6)	1 (0.6)	63 (36.6)
22		1 (0.6)	53 (30.8)	37 (21.5)	3 (1.7)	94 (54.7)
23			1 (0.6)	5 (2.9)	1 (0.6)	7 (4.1)
Total dorsal rays	1 (0.6)	12 (7.0)	99 (57.6)	55 (32.0)	5 (2.9)	

TABLE 2.—*Dorsal and anal soft-ray relation for 386 specimens of* Trachinotus falcatus

[Upper numbers in blocks represent specimens with the indicated combination; numbers in parentheses represent approximate percentage of the sample with that combination]

ANAL SOFT-RAYS	DORSAL SOFT-RAYS 17	18	19	20	21	Total anal rays
16		2 (0.5)	2 (0.5)			4 (1.0)
17	1 (0.3)	9 (2.3)	147 (38.1)	42 (10.9)		199 (51.6)
18		2 (0.5)	106 (27.5)	71 (18.4)	3 (0.8)	182 (47.2)
19					1 (0.3)	1 (0.3)
Total dorsal rays	1 (0.3)	13 (3.4)	255 (66.1)	113 (29.3)	4 (1.0)	

T. glaucus.—Elements VI–I, 19 or 20. All 39 specimens examined by Ginsburg (1952) had seven dorsal spines; 23 had 19 soft-rays and 16 had 20. All 74 specimens I examined had seven (VI–I) dorsal spines; 45 had 19 soft-rays and 29 had 20 (table 3). In the 7.8-mm. specimen (fig. 14) all soft-rays but the anteriormost and the last three are segmented. Segmentation is complete in the 11.8-mm. specimen (fig. 15). Branching has not begun by about 19 mm.; but all soft-rays except the first are branched by about 23 mm., and the first soft-ray branches between 28 and 35 mm.

Lengths

The dorsal fin possesses no lobe at sizes smaller than about 11 mm.; i.e., the anterior distal margin

is uniformly rounded. At about 11 mm., the fin margin becomes angular at the tips of soft-rays 2–4 or 5 and forms an indistinct lobe. Relative dorsal-fin lobe length increases with increased standard length at about the same rate in all species to a size of about 50 mm. At about 10–20 mm., these lengths are about 20% S.L. for *T. carolinus* and *T. falcatus* and about 22% S.L. for *T. glaucus*. By 40 to 50 mm., the lengths are about 22–25% S.L. for *T. carolinus* and about 22–29% S.L. for *T. glaucus* and *T. falcatus*. *T. carolinus* maintains a dorsal lobe length of about 24–29% S.L. from 50 mm. to above 200 mm., where there is a slight increase in relative lobe length to about 27–30% S.L. at 230–260 mm. Above 260 mm. there is a decrease in relative lobe length in *T. carolinus*, approaching about 22% S.L. in the largest specimens. Relative dorsal lobe length increases with increased standard length in *T. falcatus* and *T. glaucus* to the largest sizes examined—47% S.L. in the 216.5-mm. *T. falcatus* and 72% S.L. in the 211-mm. *T. glaucus* (appendix table 2 and fig. 20).

TABLE 3. *Dorsal and anal soft-ray relation for 74 specimens of* Trachinotus glaucus.

[Upper numbers in blocks represent specimens with the indicated combination; numbers in parentheses represent approximate percentage of the sample with that combination]

		DORSAL SOFT-RAYS		Total anal rays
		19	20	
ANAL SOFT-RAYS	16	2 (2.7)	1 (1.3)	3 (4.0)
	17	35 (47.3)	17 (23.0)	52 (70.3)
	18	8 (10.8)	11 (14.9)	19 (25.7)
Total dorsal rays		45 (60.8)	29 (39.2)	

Relative dorsal base lengths increased gradually with increased standard length to about 120 to 130 mm. in *T. carolinus* and *T. glaucus*, and increase rapidly in *T. falcatus* to about 70 mm. Below 10 mm., dorsal base lengths are about 41%, 43%, and 42% S.L. for *T. carolinus*, *T. falcatus*, and *T. glaucus*, respectively. Above 10 mm., *T. glaucus* averages the shortest, and *T. falcatus* the longest relative dorsal base lengths. By about 80 mm., the base lengths for *T. carolinus*, *T. falcatus*, and *T. glaucus* are about 53%, 57%, and 50% S.L., respectively. Beyond 80 mm., *T. falcatus* maintains a base length of about 55–59% S.L., and by 180 mm., *T. carolinus* reaches its maximum relative base length of about 57–58% S.L. The relative length of this part increases with increased standard length throughout the specimens of *T. glaucus* examined with the 211-mm. specimen possessing a dorsal base length 55% S.L. (appendix table 2 and fig. 21).

ANAL FIN

Elements

Trachinotus sp.—At 3.07 to 4.66 mm. the spines are barely discernible. No rays are present at 3.07 and 4.0 mm., but 15 soft-ray buds are evident in the 4.66-mm. specimen (figs. 1–3).

T. carolinus.—Elements II–I, 20 to 23. Ginsburg (1952) examined 346 specimens; 4 had 20 soft-rays, 127 had 21, 188 had 22, and 27 had 23. Of 172 specimens examined in this study 8 had 20 soft-rays, 63 had 21, 94 had 22, and 7 had 23 (table 1). Spines are prominent and soft-rays are developed by about 7 mm., and all but about 5 of the soft-rays are segmented (fig. 4). All soft-rays are segmented by about 10–11 mm. (fig. 5). Branching of all soft-rays but the first begins at about 17 mm. and is complete by about 21 mm. The first soft-ray branches at about 27 mm.

T. falcatus.—Elements II–I, 16 to 19. Of the 24 specimens examined by Ginsburg (1952) 15 had 17 and 9 had 18 anal soft-rays. Of 386 specimens examined in this study, 4 had 16 anal soft-rays, 199 had 17, 182 had 18, and 1 had 19 (table 2). At 5.0 mm. (fig. 8) the spines are prominent and the individual rays are discernible, but none is segmented. By 6.5–8 mm., all but 1 to 5 of the soft-rays are segmented, and by 9 mm., all anal soft-rays are segmented. Branching begins at about 13 mm. and is complete at 18 to 19 mm.

T. glaucus.—Elements II–I, 16 to 18. Ginsburg's (1952) 39 specimens were composed of 4 individuals with 16 anal soft-rays, 23 with 17, and 12 with 18. Of 74 specimens examined by me, 3 had 16 anal soft-rays, 52 had 17, and 19 had 18 (table 3). All rays but the anteriormost and the posteriormost are segmented in the 7.8-mm. specimen, and segmentation is complete in the 11.8-mm. individual (figs. 14 and 15). Branching has not begun by 19 mm., but is completed in some individuals by about 22 mm. The anterior-

most soft-ray does not branch in some specimens until about 28 mm.

Lengths

The anal-fin lobe becomes discernible at about 11 mm. Relative length of the anal-fin lobe increases with increasing standard length to about 60 mm. in *T. carolinus*. A similar increase occurs in *T. falcatus* and *T. glaucus* and continues throughout all sizes examined, except in large *T. falcatus* of 170 to 190 mm., which reach about 36% S.L., and in the largest *T. glaucus* which reach about 67% S.L. At 10–20 mm., anal-fin lobe lengths for *T. carolinus*, *T. falcatus*, and *T. glaucus* are about 18–20%, 18–22%, and 22% S.L., respectively, and by about 60 mm. they are about 22–25%, 24–26%, and 23–27% S.L., respectively. *T. carolinus* maintains a lobe length of 23–26% S.L. to about 280 mm., after which relative length decreases to about 21–24% S.L. (appendix table 2 and fig. 22).

Relative anal-fin base length increases with increasing standard length to about 100 mm. in *T. carolinus* and *T. falcatus*. Relative length increases in all sizes of *T. glaucus*, approaching 43% S.L. at 211 mm. Below 10 mm., base lengths for *T. carolinus*, *T. falcatus*, and *T. glaucus* are about 27%, 29%, and 28% S.L. respectively, and at about 100 mm., the base lengths are about 40%, 45%, and 37% S.L. *T. carolinus* and *T. falcatus* maintain relative anal-base lengths of about 38–42% S.L. and 45–47% S.L., respectively, between about 100 and 280 mm. in *T. carolinus*, and between about 100 and 216 mm. in *T. falcatus* (appendix table 2 and fig. 21).

PECTORAL FIN

Elements

Trachinotus sp.—No spines or soft-rays are evident at 3.07 and 4.0 mm. (figs. 1 and 2). Four or five soft-rays are barely discernible at 4.66 mm. (fig. 3).

T. carolinus.—Elements I, 16 to 18. Ginsburg (1952) shows the pectoral soft-ray range (compensated) as 16 to 18 on 174 specimens; 15 specimens had 16 soft-rays, 130 had 17, and 29 had 18. Of 102 specimens I examined, 14 had 16 soft-rays, 75 had 17, and 13 had 18 (table 4). At about 7 mm., all but about 4 of the soft-rays are segmented and, by about 11 mm., all rays have segmented and branching has probably begun (it is difficult to examine the innermost, or lowermost rays in small specimens, therefore error is possible in determining when these soft-rays segment or branch). Branching is complete by about 21 mm. The uppermost ray (adjacent to the spine) remains unbranched.

T. falcatus.—Elements I, 17 to 19. In examining 17 specimens, Ginsburg (1952) found two with 17 soft-rays, 14 with 18, and 1 with 19. In 78 specimens I examined, 29 had 17 soft-rays, 47 had 18, and 2 had 19 (table 4). At 5.0 mm., the individual rays are discernible, but no segmenting has occurred. By about 7 mm., all but 4 to 5 soft-rays are segmented and segmentation is complete at about 9–12 mm. Branching begins at about 14 mm., and most has occurred by 20 mm. In some individuals branching is complete by 17 mm., whereas in others it is not complete until about 45 mm.

TABLE 4.—*Pectoral soft-ray counts for* Trachinotus carolinus, T. falcatus, *and* T. glaucus

[Upper numbers in blocks represent specimens with the indicated combination; numbers in parentheses represent approximate percentage of the sample with that combination]

	PECTORAL SOFT-RAYS				
	15	16	17	18	19
T. carolinus (102 specimens)		14 (13.7)	75 (73.5)	13 (12.7)	
T. falcatus (78 specimens)			29 (37.2)	47 (60.3)	2 (2.6)
T. glaucus (71 specimens)	1 (1.4)	8 (11.3)	52 (73.2)	8 (11.3)	2 (2.8)

T. glaucus.—Elements I, 15 to 19. Thirty-six specimens examined by Ginsburg (1952) showed 2 specimens with 15 soft-rays, 5 with 16, 24 with 17, and 5 with 18. Of 71 specimens I examined, 1 had 15 soft-rays, 8 had 16, 52 had 17, 8 had 18, and 2 had 19 (table 4). All soft-rays are segmented by 11.8 mm. and branching has begun by about 16 mm. By about 19 mm., all but 3 to 10 soft-rays are branched and branching is complete by 35 to 48 mm.

Lengths at sizes below 10 mm., *T. carolinus* and *T. falcatus* have pectoral-fin lengths about 19% and 13–22% S.L., respectively. At 10–20 mm., *T. glaucus* and *T. falcatus* have reached their maximum relative pectoral-fin lengths of about 25% S.L. Relative pectoral length increases in *T. carolinus* to about 22–25% S.L. at about 70 to 80 mm. (appendix table 2 and fig.23). Relative pectoral-fin lengths are constant above

70 mm. in all species, with *T. carolinus*, *T. falcatus*, and *T. glaucus* maintaining pectoral lengths of 22–25%, 21–24%, and 21–22% S.L., respectively, to about 210–220 mm. S.L. Above 230 mm., *T. carolinus* continues a pectoral-length range of 22–25% S.L., with the largest specimen (341 mm.) possessing a pectoral length of about 19% S.L.

PELVIC FIN

Elements

Trachinotus sp.—There is no evidence of the fin at 3.07 and 4.0 mm., but at 4.66 mm. buds are discernible (figs. 1–3).

T. carolinus.—Elements I, 5. All soft-rays are segmented but none are branched before 10–12 mm. Between 12 and 16 mm. various states of branching are apparent, and after about 16 mm. branching is complete.

T. falcatus.—Elements I, 5. At 5.0 mm. the pelvic fins are minute buds, and by about 6.5 mm. the fins are small, flattened, flipperlike structures without spine or soft-rays. Spines and soft-rays are discernible at about 7 to 7.5 mm. (one 7.3-mm. specimen possesses a spine but no discernible soft-rays, the other specimens have the full complement). Segmentation begins at about this size and is completed by about 9.5 mm. Branching commences at about 11–12 mm. and is completed at 14–18 mm.

T. glaucus.—Elements I, 5. At 7.8 mm. all soft-rays are segmented, and branching is complete by 11.8 mm.

Lengths

Relative pelvic-fin length increases very rapidly in all species from about 5–11% S.L. at sizes below 10 mm. to about 16–17% S.L. at about 20 mm. *T. carolinus* maintains a pelvic length of about 15–19% S.L. to about 100 mm., after which relative pelvic length decreases gradually, becoming about 10% S.L. at sizes larger than about 290 mm. Relative pelvic length decreases gradually with an increase in standard length in *T. falcatus* at sizes above about 30 mm., becoming about 11% S.L. in specimens larger than 170 mm. *T. glaucus* maintains a pelvic length about 17% S.L. to about 70 mm., after which there is a gradual relative decrease with an increase in standard length, becoming 13% S.L. in the 211-mm. specimen (appendix table 2 and fig. 23).

CAUDAL FIN

Elements

Trachinotus sp.—At 3.07 and 4.0 mm. the caudal rays are not evident, but at 4.66 mm., six principal rays in each lobe are discernible (figs. 1–3).

T. carolinus. Rays 9+8. All principal rays are present and segmented, but none is branched at 7.2 mm. The two median caudal rays branch at about 10 mm., by about 11 mm. five or six rays in the upper lobe and about five in the lower lobe are branched, and branching is complete at 15–20 mm.

T. falcatus.—Rays 9+8. By 5–7 mm. all principal rays are present, and all but the outermost principal ray in each lobe are segmented. Segmentation is complete between 7 and 7.5 mm. Branching begins with the median caudal rays and is complete by about 12 mm.

T. glaucus.—Rays 9+8. At 7.8 mm. all principal rays are present and segmented, but none is branched. At 11.8 mm. six rays in the upper lobe and five in the lower are branched, and by 14.6 mm. seven upper rays and six lower ones are branched. All specimens larger than about 15 mm. exhibit complete branching.

Lengths

Relative caudal-fin lobe length gradually increases with an increase in standard length to about 250 mm. in *T. carolinus*. Maximum relative length of this part is undetermined in *T. falcatus* and *T. glaucus* since a continuing and moderate increase was indicated by the largest specimens examined. Below 10 mm. *T. falcatus* and *T. glaucus* exhibit caudal-fin lobe lengths about 25–35% and 33% S.L., respectively. At 10–30 mm., the lengths of this part for *T. carolinus*, *T. falcatus*, and *T. glaucus* are about 31–34%, 31–38%, and 35% S.L., respectively. Caudal-fin lobe length in *T. carolinus* increases to about 41–44% S.L. at 230 to 260 mm.; thereafter, the part decreases in relative length, approaching 35% S.L. at sizes larger than 300 mm. The four largest *T. falcatus* (172–216.5 mm.) had caudal lobe lengths 42.9–45.5%, and three of the larger *T. glaucus* (124–141.5 mm.) had caudal lobe lengths 42.8–47.3% S.L. (appendix table 2 and fig. 22).

GILL RAKERS

The complete gill-raker complement in *Trachinotus* is 7 or 8+13 or 14. This complement

is very seldom encountered, however, because of damage to the arch, destruction of rakers by parasitic isopods, and natural degeneration of gill rakers. No specimens examined had the complete complement of rakers fully developed, but they exhibited the possibility of having possessed the full complement of gill rakers at some time; i.e., they had enough rudiments or tubercles or adequate space on the ends of the arch to account for missing rakers. The separation of gill rakers from rudiments is arbitrary, the criterion used here is that a raker so shortened as to be covered with flesh and to have no appreciable flexibility is considered rudimentary.

Gill-raker degeneration usually begins at the ends of the arch and progresses toward the angle. The outermost rakers first become rudimentary and later become low tubercles. As the rudiments degenerate to tubercles other tubercles form between the gill-raker sites and masses of low tubercles form along the ends of the arch. Quite often tubercles form between fully developed rakers, especially in larger fish.

Trachinotus sp.—Gill rakers were not examined.

T. carolinus.—Rakers 7+13. Some specimens to about 310 mm. possessed the maximum number (including rudiments) on one limb of the arch. Degeneration is more pronounced on the lower limb, generally progressing with increase in size. Specimens at all sizes above 10 mm. exhibit a complement of 4 to 6 fully developed rakers in the upper arch. On the lower arch, 10- to 30-mm. specimens exhibit a range of 10 to 12 fully developed rakers (the majority have 11); at 50 to 80 mm. the range is 9–11 (half the specimens have 10); and from 80 mm. on the range is 6–10 (most specimens have 8 or 9).

T. falcatus.—Rakers 8+14. At smaller sizes (10–40 mm.) the gill-raker range is 3–8+12–14, with most specimens possessing 5 or more rakers on the upper limb. From 40 to 100 mm. the range is 5–7+10–14 (numbers evenly distributed for upper limb, but with about half the specimens with 12 rakers in the lower limb.) Above 100 mm. the range is 3–7+8–13 (with more specimens having 5 than any other count on the upper limb and with a majority having 11 or 12 on the lower limb).

T. glaucus.—Rakers 8+14. At 10 to 60 mm. the range is 3–8+9–14 (most specimens have 5 or 6 on the upper limb and 11 or 12 on the lower limb); at 60 mm. and above, it is 4–8+10–11 (about half the specimens have 6 on the upper limb and the majority have 10 on the lower limb). There is a tendency toward reduction in the number of fully developed gill rakers with increasing size of the fish.

PREOPERCULAR SPINES

Very small *Trachinotus* possess two series of conspicuous preopercular spines (figs. 1, 2, and 3). The series of preopercular-margin spines is located along the edge of the preopercle. Anterior and parallel to this is the series of preopercular-face spines. The margin series consists of three primary margin spines, at and near the angle, the middle (PMS 1) the longest and the upper (PMS 2) and lower (PMS 3) being somewhat shorter. These are followed on both limbs by preopercular-margin secondary spines. The secondary spines on the lower limb number two or three and remain fairly constant in number and relative size. The upper secondary spines are few in number at small sizes but increase in number and decrease in size as the fish grows, the result being a finely serrated margin on the upper limb during the latter stages of preopercular-spine development. This is especially true of *T. falcatus*.

The preopercular-face series consists of two or three rather obtuse spines positioned relatively the same as the primary angle spines in the margin series (PFS 1 to 3). These spines, very conspicuous in small specimens, become relatively smaller with increase in fish size and disappear at about 13 mm. The margin series remains conspicuous in fish to the larger sizes.

At about 13 mm. the preopercle begins to grow laterally, and flat, bony projections begin to radiate between and encroach upon the margin spines. As this encroachment progresses the spines are assimilated into the bony mass with the uppermost and lowermost spines disappearing first. In turn, the bony mass may radiate from the edges of the spines as the spines become a part of the preopercle. In conjunction with this process, the larger spines, primary and lower limb, become overgrown with flesh prior to bony encroachment. Any spine so covered is considered assimilated.

Other bony projections in small *Trachinotus* are a ridge over and behind the brow and short

spines near the upper end of the gill opening (figs. 1–3).

Trachinotus sp.—In the 3.07-mm. specimen, the three primary margin spines are present, superimposed by two spines of the preopercular face series. The 4.0- and 4.66-mm. fish have three primary margin spines and three primary face spines (figs. 1–3).

T. carolinus.—At 7.2 mm. there are two spines on the lower limb and one on the upper limb of the margin series, plus the angle spines. Only one face spine (PFS 3) is obvious, the other two are virtually extinct (fig. 4). By 11 mm. there are three spines on the lower limb and four on the upper, plus the angle spines, in the margin series. Two face spines (PFS 1 and 3) are present but reduced (fig. 5). The face spines are obliterated, and the margin spines reach their maximum numerical development at 12 to 13 mm. By 18 to 20 mm. all but the primary margin spines have become assimilated into the preopercle. PMS 2 and 3 are not obvious after about 24 mm. PMS 1 is the last to be assimilated, usually at about 33 mm., but is sometimes discernible to about 45 mm., and occasionally the very tip of this spine remains uncovered after the preopercular margin has grown past it.

T. falcatus.—At 5.0 mm. the primary spines and one lower limb secondary spine are found in the margin series, and the face series is comprised of three spines (fig. 8). By about 7 mm. there are two spines on the upper limb and two on the lower limb of the margin series, and three face spines are present but receding (fig. 9). By 11 mm. there are two spines on the lower limb and about five on the upper limb of the margin, and the three face spines are relatively small. In 13- to 20-mm. specimens, two or three spines comprise the lower limb margin complement, two to many spines are found on the upper limb, and the face series has disappeared (fig. 10). Preopercular encroachment and spine assimilation are rapid beyond this size, and only the primary spines are conspicuous between 20 and 30 mm. By 30 to 32 mm. all spines are assimilated.

T. glaucus.—At 7.8 mm. two spines are evident on the upper limb and none on the lower limb of the margin. Three distinct face spines are present (fig. 14). At 11.8 mm. the face spines have disappeared, and there are three margin spines on the upper limb and two on the lower (fig. 15). At 14.6 mm. three spines are present on each limb of the margin (fig. 16). After about 23 mm., PMS 1 is the only spine remaining uncovered. This spine is assimilated at about 28 to 35 mm.

BRANCHIOSTEGAL RAYS

Branchiostegal rays were counted on specimens in which the opercular flap was flared outward, thereby presenting well-spread branchiostegal membranes. In some specimens the innermost rays are very narrow and inconspicuous and are "floating" or unattached.

Trachinotus sp.—The 3.07-mm. specimen has a complement of 5 or 6+5 or 6; the 4.0- and 4.66-mm. specimens have 7+7 branchiostegal rays.

T. carolinus.—Rays, usually 7+7. Of 220 specimens examined, 195 had 7+7 branchiostegal rays, 9 had 7+8, 9 had 8+7, 6 had 8+8, and 1 had 8+9 (table 5).

T. falcatus.—Rays, usually 8+8. Of 203 specimens examined, 117 had 8+8 branchiostegal rays, 9 had 7+8, 23 had 8+7, 53 had 7+7, and 1 had 6+7 (table 6).

T. glaucus.—Rays, usually 8+8. Of 49 individuals examined, 44 had 8+8 branchiostegal rays, 3 had 7+7, 1 had 7+8, and 1 had 8+7 (table 7).

DENTITION

The following description of dentition in *Trachinotus* was obtained from specimens 20 to 60 mm. in length, but applies to all sizes in which teeth are evident. The teeth on the premaxillaries and dentaries are small, rather slender, conical, and recurved. An irregular, double row of

TABLE 5.—*Left and right branchiostegal ray relation for 220 specimens of* Trachinotus carolinus

[Upper numbers in blocks represent specimens with the indicated combination; numbers in parentheses represent approximate percentage of the sample with that combination]

		LEFT		Total right rays
		7	8	
RIGHT	7	195 (88.6)	9 (4.1)	204 (92.7)
	8	9 (4.1)	6 (2.7)	15 (6.8)
	9		1 (0.5)	1 (0.5)
Total left rays		204 (92.7)	16 (7.3)	

TABLE 6.—*Left and right branchiostegal ray relation for 203 specimens of* Trachinotus falcatus

[Upper numbers in blocks represent specimens with the indicated combination; numbers in parentheses represent approximate percentage of the sample with that combination]

		LEFT			Total right rays
		6	7	8	
RIGHT	7	1 (0.5)	53 (26.1)	23 (11.3)	77 (37.9)
	8		9 (4.4)	117 (57.6)	126 (62.1)
Total left rays		1 (0.5)	62 (30.5)	140 (69.0)	

TABLE 7.—*Left and right branchiostegal ray relation for 49 specimens of* Trachinotus glaucus

[*Upper* numbers represent specimens with the indicated combination; numbers in parentheses represent approximate percentage of the sample with that combination]

		LEFT		Total right rays
		7	8	
RIGHT	7	3 (6.1)	1 (2.0)	4 (8.2)
	8	1 (2.0)	44 (89.8)	45 (91.8)
Total left rays		4 (8.2)	45 (91.8)	

strongly recurved teeth runs most of the length of the inner edge of the premaxillaries. The remainder of the "gum" surface is covered with minute papillae. A single irregular row of slightly larger teeth of the same type, 8 to 10 teeth to each side, is located on the outer edge of each dentary for approximately half its length from the symphysis, and 2 or 3 teeth are located on each side, immediately behind the row, adjacent to the symphysis. An irregular, double row of smaller, strongly recurved teeth is located along the inner edge of the dentary for most of its length. The area between the single row and the double rows is covered with papillae.

There are 3 to 5 short, slightly recurved teeth on the head of the vomer, and a single row of about 5 slender teeth on each palatine. The teeth present on the tongue (of *T. falcatus* only) are in a narrow band on the middle of the tongue.

Some or all the teeth become overgrown with flesh and papillae as the size of the fish increases. The erratic dentition development found in some phases of this study may be effected by the preserving medium. The inherent shrinking of flesh in alcohol-preserved fish may bare teeth that would be undetectable in specimens preserved in formalin.

Trachinotus sp.—The only teeth evident at 3.07 mm. are one or two recurved ones projecting slightly forward on the anterior ends of the premaxillaries. Premaxillary teeth are also the only ones evident in the 4.0- and 4.66-mm. specimens.

T. carolinus.—Teeth are present on premaxillaries, vomer, palatines, and dentaries of the smallest specimen and all below about 20 mm. Above 20 mm. the vomerine and palatine teeth become overgrown in some specimens, although they can still be found in others up to 150 mm. At about 150 mm. all but the dentary teeth disappear and they are gone by about 170 mm.

T. falcatus.—The 5-mm. specimen has teeth on the premaxillaries, vomer, palatines, and dentaries, but has no teeth on the tongue. At 10 to 80 mm., teeth are present also on the tongue. At 80–140 mm., some specimens have no teeth on the vomer, palatines, or tongue; at 140–190 mm., teeth are found only on the tongue and dentaries; and the 216.5-mm. individual is toothless.

T. glaucus.—Teeth are present on premaxillaries, vomer, palatines, and dentaries of the 7.8-mm. specimen, and persist to at least 140 mm. The 211-mm. individual lacks teeth on the vomer.

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APPENDIX

APPENDIX TABLE 1.—*Specimens examined, by species and collection*

[Gear: S, beach seine; T, shrimp trawl; DN, dip net; P, plankton net; L, larval-fish tow net; C, commercial catch]

Collection [1]	Number of specimens	Size (mm.)	Date of capture	Gear used
Trachinotus sp.:				
BLBG:				
Gill cruise 2, Reg. Sta. 2 (26°56′ N., 79°41′ W.)	1	3.07	4-23-53	P
Combat Sta. 302 (32°10′ N., 78°56′ W.)	1	4.0	4-22-57	L
Do	1	4.66	4-22-57	L
T. carolinus:				
BLBG:				
King and Prince Beach, St. Simons Island, Ga.	1	14	4-22-53	S
Do	23	17-24	5-6-53	S
Do	10	13-16	5-20-53	S
Do	153	16-37	6-3-53	S
Do	23	14-62	6-5-53	S
Do	29	9-57	6-17-53	S
Do	240	14-68	6-18-53	S
Do	47	17-52	7-3-53	S
Do	24	21-73	7-21-53	S
Do	23	14-60	8-26-53	S
Do	14	14-34	9-9-53	S
Do	3	34-36	12-8-53	S
Do	2	14, 19	4-25-55	S
Do	2	12, 37	5-9-55	S
Do	72	13-43	5-24-55	S
Do	67	19-47	6-9-55	S
Do	73	15-94	6-22-55	S
Do	2	27, 63.5	7-22-55	S
Do	29	14-51	8-5-55	S
Do	32	21-76	9-8-55	S
Do	29	13-65	9-19-55	S
Do	19	27-35	10-5-55	S
Do	2	24, 38	11-3-55	S
Do	3	81-102	11-16-55	S
Do	2	44, 51	12-2-55	S
Do	666	11-30	5-14-56	S
Do	87	16-40	5-28-56	S
Do	106	16-62	6-11-56	S
Do	65	22-69	6-26-56	S
Do	91	12-78	7-10-56	S
Do	35	18-31	7-24-56	S
Do	25	17-65	8-8-56	S
Do	27	14-56	8-24-56	S
Do	74	13-60	9-7-56	S
Do	77	15-54	9-27-56	S
Do	31	14-42	10-11-56	S
Do	28	13.6-42.1	10-23-56	S
Do	7	22-47	11-7-56	S
Do	14	19-42	11-20-56	S
Do	30	13-18	4-16-57	S
Do	395	12-39	5-2-57	S
Do	37	12-15	5-11-57	S
Do	20	17-52	5-16-57	S
Do	83	17-76	5-31-57	S
Do	33	13-75	6-14-57	S
Do	13	13-97	7-1-57	S
Do	45	15-127.5	7-15-57	S
Do	58	13-51	7-29-57	S
Do	22	13-60	8-13-57	S
Do	11	15-28	8-27-57	S
Do	3	15-31	9-11-57	S
Do	5	20-21	9-26-57	S
Do	111	17-47	10-11-57	S
Do	3	16-21	10-25-57	S
Do	11	13-18	4-27-59	S
Do	607	12-58	5-11-59	S
Do	104	19-73	6-9-59	S
Do	84	15-63	6-23-59	S
Do	75	13-71	7-9-59	S
Do	68	14-83	7-23-59	S
Do	49	12-101	8-7-59	S
Do	9	17-78	8-21-59	S
Do	18	41-77	9-8-59	S
Do	42	18-79	9-21-59	S
Do	4	17-116	10-6-59	S
Do	2	42	10-20-59	S
East Beach, St. Simons Island, Ga.	8	14-44	8-11-53	S
Do	23	14-38	5-28-56	S
Do	3	27.2-35	6-11-56	S
Do	2	14	4-16-57	S
Do	1	51	7-9-59	S
Jekyll Island Beach, Ga.	50	12-110	7-11-56	S
Do	42	16-71	7-19-56	S

[1] See footnote at end of table.

APPENDIX TABLE 1.—*Specimens examined, by species and collection*—Continued

Collection [1]	Number of specimens	Size (mm.)	Date of capture	Gear used
T. carolinus—Cont.				
Jekyll Island Beach, Ga.	46	15-56	10-5-56	S
Do	1	12	4-16-57	S
Do	85	22-55	10-19-57	S
Do	10	13-19	4-27-59	S
Do	300	14-91	8-7-59	S
Do	29	11-66	9-8-59	S
Sapelo Beach, Sapelo Island, Ga.	1	82.5	6-10-53	S?
Commercial trawling area, Brunswick, Ga.	1	143	5-2-54	T
Do	1	101	8-17-55	T
Do	1	209	7-4-56	T
Do	1	190	7-17/20-56	T
Do	2	136.5, 150.5	7-23/24-56	T
Do	1	195	7-27-56	T
Do	4	133-160	7-31-56	T
Do	6	139-197	9-23-56	T
Do	1	165.5	3-29-57	T
Do	2	160, 166	10-22-58	T
Fort Walton Beach (Gulfarium), Okaloosa County, Fla.	2	262, 316	Spring, 1958	—
Port Canaveral, Brevard County, Fla.	1	12.1	4-28/29-57	DN
Gill cruise 3, Reg. Sta. 42 (31°57′ N., 79°16′ W.)	1	7.2	8-5-53	P
Gill cruise 8 Reg. Sta. 47 (32°40′ N., 79°00′ W.)	1	11.0	9-25-54	DN
Phillips. Beach at Marineland, St. Johns County, Fla.	7	10.1-16.7	8-12-56	S?
UF 5559. Commercial trawling area, Brunswick, Ga.	1	166.5	10-23-55	T
Inst. Jam. Kingston Harbour, Jamaica, British West Indies	1	283	6-25-57	—
ChM 31.207.3. Capers Inlet, Charleston County, S.C.	2	115, 122	9-10-31	—
Commercial catch. Indian R., Brevard County, Fla.	10	236-284	8-19-58	C
Do	20	243-341	8-20-58	C
T. falcatus:				
BLBG:				
King and Prince Beach, St. Simons Island, Ga.	2	18, 27	7-21-53	S
Do	1	14	8-26-53	S
Do	1	18	9-9-53	S
Do	5	17-20	8-6-54	S
Do	1	46.4	9-1-54	S
Do	26	18-33	10-29-54	S
Do	2	24, 28	7-22-55	S
Do	1	18	8-5-55	S
Do	15	16-23	9-6-55	S
Do	23	13-30	9-19-55	S
Do	10	18-30	10-5-55	S
Do	59	14-52	10-14-55	S
Do	4	19-34	11-3-55	S
Do	5	34-46	11-16-55	S
Do	1	22	6-11-56	S
Do	2	21, 22	6-26-56	S
Do	4	30-36	7-10-56	S
Do	1	20	7-24-56	S
Do	1	14	8-24-56	S
Do	29	12-56	9-7-56	S
Do	15	16-49	9-27-56	S
Do	4	14-22	10-23-56	S
Do	15	27-44	5-31-57	S
Do	14	24-50	6-14-57	S
Do	3	35-47	7-1-57	S
Do	7	24-31	7-9-57	S
Do	12	23-53	7-15-57	S
Do	7	21-43	7-29-57	S
Do	7	16-51	8-13-57	S
Do	12	18-51	8-27-57	S
Do	71	13-33	9-7-57	S
Do	4	21-41	9-11-57	S
Do	7	15-36	9-26-57	S
Do	79	13-102	10-11-57	S
Do	7	18-45	10-25-57	S
Do	1	18	6-4-58	S
Do	1	26	6-20-58	S
Do	2	32, 46	7-3-58	S
Do	23	15-54	8-18-58	S
Do	8	22-51	10-2-58	S
Do	15	13-65	10-16-58	S
Do	4	18-45	11-14-58	S
Do	9	20-28	6-9-59	S
Do	3	15-24	6-23-59	S

APPENDIX TABLE 1.—*Specimens examined, by species and collection*—Continued

Collection [1]	Number of specimens	Size (mm.)	Date of capture	Gear used
T. falcatus—Con.				
BLBG:				
King and Prince Beach, St. Simons Island, Ga.	4	48–59	7–23–59	S
Do	8	20–66	8–21–59	S
Do	22	23–89	9–21–59	S
Do	19	14–42	10–6–59	S
Do	1	18	11–6–59	S
East Beach, St. Simons Island, Ga.	1	20	5–28–56	S
Do	1	21	6–11–56	S
Do	2	20, 33	7–29–57	S
Do	3	27–29	7–21–58	S
Do	4	23–70	8–18–58	S
Do	40	19–57	9–2–58	S
Do	11	23–29	10–2–58	S
Do	2	37–55	11–3–58	S
Do	2	30	7–9–59	S
Do	1	16	9–8–59	S
Causeway between Jekyll Island and Brunswick, Ga.	1	17.7	10–11 57	S
Do	1	32	7–9–59	S
Jekyll Island Beach, Ga.	1	21	10–5–56	S
Do	1	24	10–19–57	S
Lewis Crab Co., Brunswick, Ga. (no data).	3	154. 5–182	5–59	------
Gill cruise 2, Reg. Sta. 40 (31°29′ N., 78°41′ W.).	1	7.7	5–5–53	DN
Gill cruise 3, Reg. Sta. 42 (31°57′ N., 79°16′ W.).	1	7.3	8–5–53	P
Gill cruise 3, Reg. Sta. 50 (31°57′ N., 78°09′ W.).	1	7.3	8–6–53	P
Gill cruise 3, Reg. Sta. 63 (33°24′ N., 76°25′ W.).	1	5.0	8–11–53	P
BLBG(M1):				
Little River, 1 mile NE Calabash, N.C.	1	59.5	7–21–56	S?
Great Egg Harbor, N.J.	1	24.1	10–6–56	S?
Indian River, Sebastian, Fla.	12	17.9–46.6	11–7–56	S?
USNM 49635: Woods Hole, Mass.	4	20.2–33.6	8–14–99	------
USNM 143935: Katama Bay, Mass.	2	17.7, 20.6	7–27–15	------
USNM 67890: Bay near Ocean View, Va.	1	64.5	9–98	------
USNM 74292: Cape Lookout, N.C.	1	44.9	7–12	------
USNM 111763: Fort Macon, N.C.	1	27.3	6–30–32	------
USNM 122646: Port au Prince market, Haiti.	1	172	1943	------
USNM 50126: Mayaguez, Porto Rico.	1	132	1–19–99	------
USNM 73745: Do	3	26.4–42.9	1–19–99	------
USNM 111762: Key West, Fla., near Slaughter House.	4(of 15)	17–84	10–13–19	------
USNM 26585: Key West, Fla.	1	216.5	1880	------
USNM 125517: Tampa market, Fla.	1	125.5	11–7–96	------
USNM 26596: Cedar Key, Fla.	1	63.5	1880	------
USNM 185075: Do	1	42.1	10–12–47	------
USNM 116840: Tortugas, Fla.	3	32.5–64.5	----------	------
USNM 143940: Oso bridge, Corpus Christi Bay, Tex.	1	133 5	8–26–26	------
USNM 143939: Corpus Christi, Tex.	2	26.1, 35.6	10–14/29–26	------
USNM 80100: Fox Bay, Panama.	3	32.2–42.5	1–3–11	------
USNM 44703: Central America (probably from Atlantic).	1	127.5	1893	------
USNM 76319: Porto Seguiro, Brazil.	2	74, 85	----------	------
UF C–6–1256–1: Plantation Key, Monroe County, Fla.	3	12 3–15.7	6–12–56	------
Inst. Jam.: Lazaretto Cairn, Jamaica, near Kingston.	1	57.0	6–16–57	------
ChM 31.267: Mount Pleasant, E. Frampton, S.C.	1	136.5	11–11–31	------
ChM 31.207.12: Capers Inlet, S.C.	15	21–48.9	9–10–31	------
UG 378: Sapelo Island, Ga.	1	85.5	9–4–54	------
BU: M/V *Delaware* (37°30′ N; 68°10′ W.).	1	11.7	7–11–57	DN
T. falcatus—Con.				
Phillips:				
Fort Pierce, Fla.	40	9.8–28.6	8–29–55	------
Do	45	23–66.5	10–8–55	------
Bahia Honda, Fla.	4	76–103	4–15–56	------
Marineland Beach, Fla.	1	38.1	8–12–56	------
Largo Sound, Fla.	35	18.4–46.6	7–15–56	------
Marco Beach, Fla.	1	89.5	7–16–56	------
Crandon Park, Miami, Fla.	4	9.1–18.8	5–24–57	------
Do	1	9.3	7–9–57	------
Do	2	8.5, 9	5–1–56	------
Do	4	8.3–9.5	6–12–56	------
Do	2	10.4, 10.7	1–28–57	------
Do	32	7.2–10.6	2–7–57	------
Do	14	6.7–11.1	2–8–57	------
Do	5	8.5–11.5	4–1–57	------
Do	11	6.7–11.5	4–24–57	------
Do	2	9.9, 10	5–1–57	------
Do	3	6.4–9.8	9–1–57	------
Do	1	8.9	9–2–57	------
Do	1	7.6	4–15–58	------
Bear Cut, Miami, Fla.	1	7.6	8–17–54	------
Do	1	11.3	3–23–57	------
Virginia Key, Miami, Fla.	1	8.1	9–17–54	------
Vero Beach, Fla.	1	7.9	7–21–56	------
Do	1	8.9	7–25–56	------
Do	1	8.4	7–31–56	------
Do	9	6.4–12.1	8–12–56	------
Do	1	8.9	8–14–56	------
T. glaucus;				
BLBG:				
King and Prince Beach, St. Simons Island, Ga.	1	28.9	10–29–54	S
Do	2	35.8, 39.4	9–7–56	S
Do	2	23.9, 24	9–27–56	S
Do	1	23.3	11–20–56	S
Do	3	48.5–61	10–11–57	S
Do	1	19.4	10–25–57	S
Do	1	26.2	11–14–58	S
Do	1	60.0	8–7–59	S
UF (uncataloged):				
Open Gulf beach, 5 km. south Veracruz, Mocambo, Mexico.	4	76.5–124	1–20/21–58	------
Beach 5 miles W. Nassau, New Providence Island, Bahamas.	21	16.6–110	7–5–58	------
Do	1	128	8–11–56	------
UF 5908:				
Flagler Beach, Flagler County, Fla.	7	36–50.5	10–2–56	------
Inst. Jam.:				
Lucea, Jamaica	1	211	9–30–51	------
Kingston market, Jamaica	1	141.5	4–24–59	------
ChM:				
Old Collection; S.C.	1 (of 2).	139	----------	------
Phillips:				
Bahia Honda Key, Fla.	5	71.5–89	4–15–56	S
Crandon Park, Miami, Fla.	1	11.8	2–8–57	------
Seaquarium Boat Dock, Miami, Fla.	1	7.8	2–8–58	------
USNM 125672. Buzzards Bay, Mass.	1	65	9–22–97	------
USNM 62699. St. Augustine, Fla.	4	35.3–45.5	11–18–08	------
USNM 50100. Aquadilla, Porto Rico.	1	110	----------	------
USNM 73744. Mayaguez, Puerto Rico.	1	42.4	1–20–99	------
USNM 111767. Key West, Fla.	1	40.5	10–13–19	------
USNM 68595. Dry Tortugas, Fla.	1	63	----------	------
USNM 61127. Tortugas, Fla.	4	40–45	----------	------
USNM 143952. Tortugas, Fla.	2	43, 65	11–25–19	------
USNM 143953. Louisiana	1	14.6	----------	------
USNM 143954. Aransas Pass, Tex.	4	73–88	10–2/11–26	------
USNM 123068. Cape San Roman, Gulf of Venezuela.	3	24.7–85	4–2–25	------

[1] Abbreviations explained, page 189.

APPENDIX TABLE 2.—*Measurements of selected body proportions for* Trachinotus *spp., expressed as percent of standard length*

Standard length (mm.)	Percent of standard length										
	Head length	Eye diameter	Body depth	Dorsal fin		Anal fin		Pectoral fin length	Pelvic-fin length	Caudal-fin lobe length
				Lobe length	Base length	Lobe length	Base length			
Trachinotus sp.										
3.07	39.1	11.0	18.2	-----	-----	-----	-----	-----	-----	-----
4.0	41.5	13.2	19.2	-----	-----	-----	-----	-----	-----	-----
4.66	33.8	11.2	20.2	-----	-----	-----	-----	-----	-----	-----
T. carolinus:										
7.2	39.5	13.1	32.0	-----	41.4	-----	26.9	18.9	9.7	-----
10.1	38.8	13.5	32.0	-----	46.3	-----	32.8	24.4	12.5	32.8
10.3	37.0	13.5	31.7	-----	46.7	-----	30.2	22.8	14.5	33.5
10.6	37.9	13.1	30.5	-----	43.2	-----	31.4	24.5	14.7	32.9
11.0	37.0	12.7	34.7	17.1	46.4	-----	29.2	20.6	15.1	33.5
11.1	37.0	12.1	39.0	-----	43.6	-----	32.2	20.9	16.1	33.2
11.5	37.2	12.4	33.8	-----	46.0	-----	30.5	23.0	13.6	33.9
11.8	36.5	12.4	30.1	19.4	45.0	-----	30.2	20.9	13.5	33.0
11.8	35.6	12.4	28.7	-----	45.0	20.8	29.5	20.1	15.6	33.0
12.0	38.0	13.3	34.7	-----	45.8	18.8	29.9	21.3	17.1	33.2
12.1	39.8	12.8	33.2	19.8	43.8	17.6	29.9	21.4	13.7	34.0
13.0	35.9	12.2	32.6	18.3	45.4	17.4	30.8	21.2	14.9	33.0
13.2	37.9	12.5	31.6	19.9	46.2	18.6	29.6	23.6	15.9	33.4
14.1	36.2	12.4	31.4	17.5	43.3	17.4	29.8	20.9	14.9	33.2
15.8	35.4	11.7	33.6	19.1	46.8	18.2	31.6	21.9	15.6	31.6
16.7	37.8	12.1	34.1	20.4	47.3	18.3	31.7	21.8	16.3	32.9
18.9	35.4	10.8	33.9	20.4	47.1	19.0	30.6	-----	15.6	32.8
21.6	37.5	10.4	35.2	20.2	45.9	19.9	29.6	19.9	15.9	32.4
24.6	35.4	10.1	35.8	20.0	47.2	19.2	30.1	20.7	16.0	31.3
25.7	-----	-----	32.7	21.0	-----	20.6	-----	19.1	17.1	34.2
27.2	32.4	9.5	38.2	21.4	49.7	19.9	32.7	19.1	14.7	33.1
29.3	33.2	10.2	31.4	22.1	46.5	21.2	30.0	20.8	18.5	33.8
30.6	-----	-----	38.0	21.2	-----	22.3	-----	20.3	17.3	35.3
31.3	-----	-----	34.9	19.8	-----	20.8	-----	19.5	15.7	34.6
31.7	31.9	8.2	35.7	21.4	45.2	20.5	30.3	21.1	16.8	31.6
31.9	-----	-----	36.7	22.6	-----	22.0	-----	21.0	16.3	35.4
33.2	-----	-----	35.6	21.7	-----	22.3	-----	21.4	19.3	34.7
33.5	30.5	9.8	33.7	22.7	48.4	21.5	31.4	20.6	15.8	33.8
33.7	-----	-----	34.7	22.8	-----	23.4	-----	21.0	17.2	-----
35.5	32.7	9.7	41.1	21.0	49.0	20.9	33.5	17.2	14.4	31.8
37.4	-----	-----	35.6	22.7	-----	24.0	-----	21.7	16.9	34.5
37.5	-----	-----	40.0	-----	-----	22.7	-----	21.4	15.2	35.8
38.0	31.3	9.7	34.8	21.3	50.0	21.8	33.2	20.5	-----	33.2
40.0	33.0	9.3	40.3	25.3	50.5	20.2	34.5	20.2	16.2	31.5
40.0	-----	-----	44.3	21.2	-----	24.5	-----	22.3	14.5	37.5
42.1	30.6	8.9	38.3	22.6	50.4	21.4	33.4	21.4	14.7	34.2
43.9	-----	-----	39.4	25.8	-----	23.0	-----	22.4	16.4	38.7
44.0	-----	-----	40.5	26.2	-----	25.0	-----	21.8	17.8	36.4
44.0	-----	-----	37.8	22.8	-----	20.7	-----	20.9	17.3	34.0
45.1	35.5	10.2	36.2	24.2	47.6	21.0	32.8	21.3	18.6	33.9
46.4	-----	-----	37.5	23.6	-----	21.6	-----	25.0	16.8	38.4
47.4	-----	-----	40.6	25.4	-----	23.2	-----	23.4	17.1	38.6
48.3	32.2	9.3	40.0	23.4	-----	21.8	36.5	20.5	15.7	37.9
50.0	-----	-----	40.8	25.6	-----	24.0	-----	20.0	16.8	36.0
51.0	-----	-----	39.4	24.9	-----	23.7	-----	23.0	16.7	36.7
52.0	31.6	9.3	43.5	24.2	53.5	22.8	36.9	24.6	14.8	34.2
53.5	-----	-----	35.4	23.0	-----	22.0	-----	20.9	15.7	35.5
55.5	-----	-----	38.0	25.6	-----	22.7	-----	21.3	16.8	35.2
56.0	-----	-----	41.6	23.6	-----	25.0	-----	22.4	17.2	37.5
56.5	32.4	10.1	37.7	24.0	50.6	22.6	34.3	22.0	16.3	36.3
58.5	-----	-----	44.0	27.9	-----	25.8	-----	24.0	17.8	40.2
59.0	-----	-----	39.9	24.3	-----	22.2	-----	20.9	15.8	35.4
61.5	-----	-----	43.4	23.9	-----	23.7	-----	22.5	16.4	39.6
63.5	32.8	9.8	46.9	26.8	53.7	25.0	38.3	24.4	18.4	39.2
64.0	-----	-----	41.0	23.8	-----	21.7	-----	20.8	16.9	32.7
65.0	-----	-----	38.5	24.0	-----	23.4	-----	21.6	15.7	36.5
66.0	-----	-----	39.5	23.8	-----	24.0	-----	21.7	17.2	37.6
67.0	-----	-----	39.9	25.0	-----	22.8	-----	21.4	16.0	37.6
67.5	-----	-----	40.6	24.9	-----	22.5	-----	21.0	15.3	37.0
68.0	-----	-----	39.6	24.7	-----	22.6	-----	21.0	16.2	36.5
68.5	31.4	8.6	41.7	26.4	51.4	24.2	36.3	23.8	15.5	38.0
69.0	-----	-----	42.2	25.4	-----	22.4	-----	21.3	16.0	36.0
69.5	-----	-----	42.3	25.3	-----	23.4	-----	21.3	16.7	36.4
72.5	-----	-----	42.6	27.6	-----	24.7	-----	23.3	16.0	38.2
74.5	-----	-----	41.8	25.1	-----	22.8	-----	21.6	15.8	35.8
77.5	31.9	9.2	46.2	27.1	55.0	23.4	38.6	25.3	14.1	39.7
77.5	-----	-----	48.5	28.2	-----	25.2	-----	24.2	15.7	-----
82.5	30.7	7.8	46.2	24.9	52.5	24.6	38.6	22.2	14.0	35.2
83.5	-----	-----	42.8	24.3	-----	23.8	-----	21.4	15.5	38.1
84.5	-----	-----	46.0	24.3	-----	24.0	-----	22.4	15.5	36.2
85.5	-----	-----	42.8	24.2	-----	22.8	-----	21.0	14.8	35.9
88.0	30.3	9.9	45.9	27.4	54.7	29.9	38.8	26.3	16.6	40.6
91.0	-----	-----	42.5	26.8	-----	23.6	-----	22.5	15.8	37.6
91.0	-----	-----	41.7	26.8	-----	23.2	-----	22.5	15.9	36.6
91.5	-----	-----	42.7	27.4	-----	23.8	-----	22.8	15.4	39.8
91.5	-----	-----	42.6	24.6	-----	23.8	-----	22.8	15.2	38.2
93.0	-----	-----	41.9	24.6	-----	22.6	-----	23.4	15.6	38.0
96.5	31.3	8.0	46.8	25.2	54.0	24.1	38.0	24.0	14.7	37.8

APPENDIX TABLE 2.—*Measurements of selected body proportions for* Trachinotus *spp., expressed as percent of standard length*—Continued

Standard length (mm.)	Percent of standard length									
	Head length	Eye diameter	Body depth	Dorsal fin		Anal fin		Pectoral fin length	Pelvic-fin length	Caudal-fin lobe length
				Lobe length	Base length	Lobe length	Base length			
T. carolinus—Con.										
99.0	-----	-----	44.1	26.3	-----	24.2	-----	23.4	14.9	36.2
101.0	31.4	8.2	48.7	27.0	54.5	23.6	40.0	24.4	15.0	41.4
108.5	31.2	8.1	48.0	25.7	53.0	24.6	39.8	24.7	17.6	38.6
115.0	28.8	7.9	49.6	27.9	54.0	25.8	40.5	23.6	13.8	-----
119.5	-----	-----	46.3	26.2	-----	23.3	-----	23.6	14.3	37.4
122.0	27.6	7.0	50.0	29.1	55.8	-----	40.0	23.9	15.0	39.9
127.5	27.7	6.7	47.8	23.9	56.1	24.9	41.6	24.0	15.6	38.6
133.0	27.9	6.6	47.4	27.1	55.3	25.5	39.1	23.4	-----	38.4
136.5	27.8	6.7	46.8	30.0	54.6	22.3	41.4	22.0	13.5	35.9
139.0	28.2	7.2	49.6	28.8	56.9	25.0	41.4	25.3	14.5	42.0
143.0	28.3	6.9	49.3	27.4	55.3	24 0	40.2	24.6	13.5	42.3
144.0	28.6	-----	48.7	24.7	54.5	24.4	40.3	23.4	13.2	37.0
148.0	-----	-----	45.7	25.4	-----	23.4	-----	22.4	12.6	37.7
149.0	-----	6.4	46.9	23.4	-----	23.3	-----	22.6	13.1	37.8
150.5	26.3	6.6	46.8	28.6	56.9	23.6	41.2	22.4	14.3	39.0
157.0	26.6	6.6	45.8	28.5	56.1	25.6	42.0	25.1	12.9	38.2
158.0	27.0	6.7	47.5	25.9	55.7	26.0	41.2	23.7	13.5	38.9
160.0	25.4	5.7	45.6	25.4	55.7	25.6	39.4	23.8	13.1	36.8
160.0	28.0	7.4	46.9	26.0	55.0	24.8	39.4	23.5	13.7	40.0
165.5	25.4	6.5	45.3	26.6	56.3	23.1	41.0	24.4	14.4	41.7
166.0	28.6	7.4	46.7	30.7	54.9	28.1	38.0	24 9	13.7	41.0
166.5	28.6	8.0	49.3	23.7	54.7	23.0	40.8	23.3	14.0	38.1
177.0	25.2	5.9	49.4	26.3	58.0	24.5	40.5	23.8	11.8	39.5
182.0	25.6	6.0	55.0	27.3	57.0	25.5	41.2	24.0	13.5	40.7
183.5	26.6	6.3	46.9	27.0	56.8	24.8	39.8	23.6	13.1	40.0
190.0	26.0	6.0	46.3	25.6	56.9	24.2	41.0	24.4	13.5	41.8
195.0	28.8	7.1	45.1	24 7	54.0	27.4	38.7	25.0	12.5	-----
197.0	26.3	6.2	50.3	25.4	56.4	24 2	39.6	23.2	12.6	38.0
209.0	27.2	6.7	44.5	26.6	56.8	23.8	40.5	23.2	13.3	40.6
236.0	26.7	6.8	44.5	30.5	-----	25.8	-----	25.4	12.3	41.5
240.0	26.0	6.8	44.6	25.0	-----	23.0	-----	24.2	11.6	42.5
240.0	25.2	6.4	44.2	28.8	-----	23.6	-----	22.9	11.6	42.1
243.0	25.7	6.3	44.9	25.9	-----	21.6	-----	23.4	11.5	40.3
243.0	25.9	-----	47.0	29.6	-----	25.3	-----	24.4	11.9	40.6
248.0	26.0	7.3	46.4	27.6	-----	25.0	-----	24.2	12.5	46.5
248.0	25.6	-----	45.2	29.9	-----	24.8	-----	24.0	11.5	40.7
251.0	25.5	-----	45.3	31.0	-----	26.3	-----	25.5	12.1	42.3
252.0	25.4	-----	45.7	27.8	-----	24.8	-----	25.0	12.1	45.6
261.0	25.6	-----	44.1	28.6	-----	24.0	-----	23.8	11.6	41.7
262.0	26.7	6.0	45.4	26.3	57.3	24.4	41.7	22.9	11.0	43.7
264.0	25.2	6.0	44.3	26.2	-----	26.2	-----	23.3	11.9	40.4
264.0	26.5	-----	44.0	26.9	-----	23.3	-----	23.3	12.2	44.3
267.0	24.7	-----	43.7	27.7	-----	23.6	-----	23.8	11.7	-----
270.0	25.6	-----	49.3	24.1	-----	23.7	-----	23.5	11.5	39.9
272.0	25.9	-----	46.9	24.8	-----	23.5	-----	23.2	11.0	39.0
277.0	24.4	6.5	43.0	24.2	-----	23.8	-----	23.8	11.6	40.8
277.0	25.1	-----	40.8	27.0	-----	24.0	-----	23.1	11.9	40.0
278.0	23.8	-----	44.6	23.2	-----	21.8	-----	23.0	11.5	39.6
280.0	25.7	-----	42.8	26.8	-----	23.6	-----	23.9	11.4	39.4
280.0	23.9	-----	44.6	26.8	-----	26.4	-----	22.8	11.2	40.6
281.0	24.8	-----	43.3	26.3	-----	24.9	-----	23.8	11.5	41.7
283.0	28.8	7.6	43.0	28.8	54.0	26.5	40.2	25.8	12.7	40.7
284.0	25.0	-----	45.4	25.5	-----	22.5	-----	22.0	10.7	39.9
292.0	25.0	-----	42.5	25.3	-----	23.0	-----	22.8	11.0	40.0
294.0	24.5	-----	43.2	26.7	-----	21.4	-----	23.0	10.8	39.6
297.0	-----	-----	39.6	20.9	-----	21.6	-----	22.6	10.9	38.4
297.0	24.8	-----	42.4	25.6	-----	23.6	-----	22.6	10.8	40.0
310.0	24.5	6.5	42.6	25.5	-----	22.4	-----	23.0	11.0	38.8
310.0	24.8	5.5	42.6	24.8	-----	24.7	-----	22.9	10.2	38.4
316.0	24.8	5.9	39.7	-----	54.9	-----	37.4	20.7	10.3	34.0
324.0	24.7	5.3	44.7	23.2	-----	21.6	-----	23.0	10.9	38.0
341.0	23.5	-----	39.6	22.0	-----	20.5	-----	19.6	10.0	35.8
T. falcatus:										
5.0	41.8	15.8	30.4	-----	42.0	-----	24.0	13.0	-----	24.6
6.7	39.0	14.3	32.9	-----	42.7	-----	29.6	-----	5.4	-----
7.3	42.4	14.4	36.0	-----	44.8	-----	31.0	21.5	6.3	-----
7.3	43.6	15.0	35.4	-----	43.6	-----	29.0	17.0	7.9	-----
7.3	38.5	15.5	39.4	-----	42.0	-----	28.1	-----	8.1	-----
7.3	38.0	14.0	40.5	-----	37.7	-----	29.2	-----	10.4	-----
7.7	43.2	16.4	44.2	-----	47.9	-----	29.0	-----	10.0	35.2
9.0	39.5	14.8	37.0	-----	43.9	-----	30.2	-----	9.7	-----
9.8	39.0	13.9	39.8	17.4	-----	18.2	-----	22.6	11.2	31.2
10.7	-----	-----	40.5	18.2	-----	19.1	-----	23.8	14.3	33.3
10.9	37.3	12.5	42.0	21.0	-----	19.4	-----	23.8	14.0	35.0
11.1	39.0	13.7	44.3	20.8	46.0	19.0	31.4	23.3	12.0	34.6
11.3	36.8	12.7	42.0	19.5	-----	18.9	-----	21.8	14.2	33.8
11.5	39.8	12.5	42.8	18.4	-----	17.0	-----	22.9	13.3	34.7
11.7	42.8	15.2	40.6	20.4	-----	21.8	-----	23.9	15.2	34.1
12.1	38.6	12.6	41.5	19.7	-----	17.5	-----	22.5	11.9	33.6
12.1	37.2	12.6	46.2	-----	-----	18.3	-----	20.3	13.3	35.8
12.5	38.7	13.6	48.8	18.3	-----	19.1	-----	23.8	14.2	35.3
12.6	40.5	14.1	46.0	20.9	-----	20.2	-----	24.3	15.5	37.1

APPENDIX TABLE 2.—*Measurements of selected body proportions for* Trachinotus *spp., expressed as percent of standard length*—Continued

Standard length (mm.)	Percent of standard length									
	Head length	Eye diameter	Body depth	Dorsal fin		Anal fin		Pectoral fin length	Pelvic-fin length	Caudal-fin lobe length
				Lobe length	Base length	Lobe length	Base length			
T. falcatus—Con.										
12.7	37.4	13.4	41.7	------	------	18.7	------	24.1	14.0	35.4
12.8	41.4	13.9	46.9	20.5	------	21.2	------	23.9	13.9	35.2
13.1	39.7	13.0	48.1	18.8	------	19.5	------	23.4	14.9	32.4
13.2	40.2	14.2	47.0	19.3	------	19.3	------	23.8	13.5	34.1
13.3	40.6	13.4	40.0	19.8	------	19.2	------	21.7	16.6	33.8
13.5	38.5	13.9	48.8	21.4	------	21.4	------	23.9	15.1	34.6
13.6	36.4	12.5	------	16.5	47.8	18.2	33.3	21.8	15.6	31.1
13.6	38.9	12.4	47.0	19.3	------	20.6	------	23.1	14.5	34.9
13.7	40.1	13.7	48.2	19.2	------	19.8	------	22.9	14.9	34.1
13.9	38.2	12.8	48.2	22.0	------	20.1	------	24.4	14.7	34.8
14.0	37.8	12.7	42.9	19.4	------	20.0	------	23.1	13.9	33.9
14.6	41.1	15.1	50.0	19.2	------	21.0	------	24.4	15.7	33.7
14.8	39.2	13.2	44.6	20.0	------	20.0	------	23.5	17.2	34.5
14.8	40.6	14.3	52.0	19.5	------	18.4	------	23.5	14.9	34.5
15.2	38.2	13.4	44.8	21.8	------	21.2	------	24.5	15.7	34.9
15.2	40.2	13.9	53.3	20.6	------	21.8	------	22.9	15.7	36.8
15.3	38.6	12.2	49.0	21.6	------	20.0	------	23.3	14.4	34.6
15.4	40.3	13.4	51.3	21.2	49.3	22.0	36.4	24.4	16.6	35.1
15.4	38.9	14.7	41.5	21.0	------	19.9	------	24.2	16.0	35.1
15.5	38.7	14.4	48.4	19.8	47.0	20.0	33.5	24.2	15.9	34.8
15.6	41.0	13.6	53.9	20.7	------	20.7	------	23.9	15.8	36.5
15.9	------	------	52.7	19.2	------	20.3	------	23.5	15.0	34.0
16.2	38.9	13.1	50.0	22.0	------	21.4	------	24.6	16.2	36.4
16.5	37.6	12.4	50.3	20.0	------	20.0	------	23.2	14.9	33.9
16.5	37.6	13.4	49.7	20.0	------	20.0	------	23.2	14.4	33.3
16.8	38.6	12.6	44.0	18.7	------	20.4	------	23.2	16.7	33.9
17.0	40.0	14.6	47.0	22.0	48.8	19.0	34.7	24.5	12.4	35.9
17.1	38.5	12.9	51.0	19.8	------	19.8	------	22.8	15.9	33.9
17.3	37.5	12.8	43.4	19.1	------	19.6	------	23.5	15.7	34.1
17.4	35.0	11.7	45.4	20.4	------	20.0	------	22.0	15.1	33.9
17.5	40.6	13.1	46.8	21.8	------	19.9	------	22.8	18.5	34.3
17.5	37.6	13.6	50.3	20.3	------	19.9	------	23.8	16.0	33.1
17.7	39.6	13.3	52.5	18.2	49.7	18.8	37.3	22.6	15.5	37.3
17.7	39.0	13.9	55.4	22.5	50.3	22.5	37.3	25.4	15.4	33.3
17.9	39.1	14.2	52.5	21.3	------	22.8	------	24.2	16.1	36.3
17.9	38.5	14.7	45.8	23.2	------	------	------	23.7	15.6	35.8
18.2	40.1	14.3	44.5	22.5	47.8	21.8	34.6	24.5	16.2	34.6
18.4	34.2	12.4	34.2	19.8	------	18.9	------	21.2	15.2	31.5
18.5	39.5	11.9	42.7	19.7	------	19.2	------	23.4	15.1	34.6
18.8	35.6	14.9	52.1	20.7	50.0	22.1	37.8	23.2	16.7	33.0
18.8	40.9	12.9	53.1	21.6	------	21.7	------	23.9	14.6	34.6
19.0	40.0	13.4	50.5	20.5	------	20.5	------	22.8	16.1	35.3
19.2	36.4	12.4	44.7	19.9	------	19.0	------	22.1	14.2	33.3
19.6	39.8	12.1	45.4	19.9	------	19.6	------	21.4	16.5	32.7
19.6	35.2	13.0	43.4	20.8	------	20.4	------	22.1	15.6	34.2
19.7	37.5	13.8	54.3	18.9	------	21.1	------	25.0	16.4	35.5
20.1	37.3	13.6	52.7	21.0	------	20.2	------	23.2	15.2	34.8
20.5	35.6	11.6	45.9	19.5	------	21.1	------	23.2	16.1	33.7
20.6	36.9	13.6	58.8	22.8	52.0	21.0	37.8	23.1	16.5	29.1
20.9	37.3	13.8	52.6	------	51.8	20.7	38.7	17.8	13.4	36.4
21.0	35.2	12.4	48.6	20.2	49.1	21.6	36.2	23.4	16.0	34.8
21.2	33.5	11.2	43.9	20.0	------	19.5	------	21.2	14.8	31.6
21.4	39.2	14.3	58.5	23.8	------	24.8	------	23.4	15.5	37.9
21.4	37.3	12.3	46.2	19.8	------	19.8	------	21.8	15.8	34.6
21.5	37.7	13.8	51.2	20.4	------	20.9	------	23.7	16.2	34.4
21.8	39.0	14.0	52.8	23.8	------	23.8	------	23.9	17.1	37.2
22.0	34.5	12.0	51.0	19.2	------	21.2	------	24.5	16.2	36.4
22.7	36.6	13.1	53.0	20.2	------	20.2	------	22.9	15.7	33.9
22.7	36.1	12.0	45.9	20.9	------	20.6	------	24.2	15.3	35.2
22.8	35.5	12.8	54.0	25.4	50.6	24.5	38.2	24.1	19.2	34.6
22.9	37.5	13.7	53.8	23.2	------	23.1	------	24.0	15.9	36.7
23.3	37.7	12.7	48.5	24.0	50.8	23.6	37.4	22.3	16.5	35.6
23.4	36.7	12.0	57.8	22.8	------	21.8	------	25.2	15.6	37.6
23.4	37.2	13.4	45.0	21.0	------	20.9	------	22.2	16.7	35.0
23.6	36.0	12.2	46.7	21.6	------	21.2	------	23.3	16.2	34.3
23.7	37.2	12.2	56.1	21.5	------	22.8	------	23.6	15.0	34.2
23.8	34.0	11.4	45.8	20.6	------	19.9	------	21.4	14.6	33.2
24.3	37.0	11.5	58.0	22.6	52.8	19.5	38.7	25.9	14.7	39.1
24.3	35.8	14.6	49.0	21.0	------	21.4	------	21.4	16.4	31.7
24.6	33.3	10.8	51.2	22.4	53.3	20.7	38.6	22.4	16.7	36.6
25.1	37.1	12.9	47.4	21.5	------	21.9	------	23.5	14.9	35.1
26.1	34.0	11.1	58.3	22.6	52.5	20.3	38.7	22.6	14.0	34.5
26.1	33.3	11.1	52.5	19.8	------	22.2	------	21.8	15.6	33.3
26.1	33.3	11.7	46.4	20.3	------	22.6	------	20.3	15.3	33.0
26.2	35.5	12.0	44.0	22.9	------	21.8	------	22.5	15.9	33.6
26.4	35.2	12.4	49.7	22.0	50.0	22.7	36.8	23.1	16.1	35.2
26.4	35.9	12.8	51.2	24.6	50.0	------	35.6	24.2	15.4	38.6
26.4	34.8	12.6	51.9	21.6	------	22.3	------	24.2	12.9	34.1
26.4	37.1	13.8	59.5	24.2	------	23.0	------	22.3	18.0	37.5
26.5	32.8	10.9	47.6	20.0	------	19.2	------	22.3	14.7	32.5
26.9	32.0	11.0	47.6	20.8	------	20.4	------	21.2	15.1	33.1
27.2	37.9	12.8	54.5	22.4	------	22.4	------	23.5	17.5	36.0

APPENDIX TABLE 2.—*Measurements of selected body proportions for* Trachinotus *spp., expressed as percent of standard length*—Continued

Standard length (mm.)	Percent of standard length									
	Head length	Eye diameter	Body depth	Dorsal fin		Anal fin		Pectoral fin length	Pelvic-fin length	Caudal-fin lobe length
				Lobe length	Base length	Lobe length	Base length			
T. falcatus—Con.										
27.2	33.4	12.5	51.6	22.0	------	22.0	------	21.7	15.9	33.5
27.2	37.5	11.3	46.3	24.6	------	25.7	------	25.4	15.6	38.2
27.3	35.8	12.4	60.9	22.4	55.4	23.4	41.4	22.0	15.9	34.1
27.6	36.2	12.3	47.1	19.6	------	20.3	------	23.2	14.5	32.2
28.0	34.2	10.9	47.2	20.7	------	20.3	------	21.1	14.9	33.6
28.6	33.5	11.0	47.6	20.3	------	19.2	------	20.3	14.8	31.5
28.8	34.8	11.5	52.9	22.6	50.8	20.8	39.3	22.6	14.0	37.2
28.9	35.0	11.4	44.0	20.4	------	19.4	------	20.8	15.8	33.6
28.9	35.0	12.3	45.7	21.1	------	20.8	------	21.5	14.4	33.6
29.2	35.6	11.9	60.4	24.3	52.8	21.6	40.4	23.6	16.0	37.0
29.2	37.4	13.7	47.0	22.2	------	------	------	24.0	16.3	33.6
29.4	32.6	10.4	48.6	20.0	------	20.4	------	21.1	14.7	31.6
29.6	35.2	12.6	58.8	24.4	------	23.3	------	------	15.2	37.2
29.6	34.5	12.0	47.3	21.2	------	21.6	------	23.3	14.9	35.1
30.5	35.1	11.5	49.5	22.3	49.9	22.6	37.4	22.6	13.9	35.1
31.2	35.3	11.4	46.5	20.5	------	20.8	------	21.5	15.5	32.7
32.2	33.6	12.4	56.5	------	52.0	21.4	39.8	21.1	15.0	35.4
32.4	33.4	11.0	49.1	23.4	50.3	22.8	38.0	21.7	17.3	37.0
32.5	33.9	12.3	47.1	23.7	51.5	22.4	36.4	22.2	15.4	36.0
32.5	36.1	12.3	46.8	23.0	------	23.6	------	23.4	14.8	36.3
33.1	34.1	11.5	50.5	24.5	51.5	20.8	37.5	23.0	14.6	34.4
33.1	34.8	12.0	49.6	21.7	------	24.2	------	22.7	16.0	34.1
33.3	34.6	11.2	48.7	22.8	------	22.8	------	23.4	15.9	------
33.6	35.4	11.6	61.0	22.6	52.7	22.0	42.3	24.1	15.8	37.8
34.4	35.8	12.3	52.4	25.6	51.2	23.8	38.7	23.0	15.7	33.4
35.4	33.9	10.3	47.2	23.2	------	22.8	------	22.6	15.0	35.3
35.6	32.3	11.4	63.8	26.4	54.5	------	41.3	23.6	16.0	38.5
35.6	34.6	12.2	67.6	24.7	56.5	21.3	42.7	26.1	16.6	36.8
35.9	35.7	12.1	60.0	23.7	------	22.6	------	22.8	14.8	35.4
35.9	32.3	11.3	48.7	24.2	------	25.4	------	23.1	15.6	35.7
36.2	33.4	10.6	60.0	23.8	------	23.4	------	23.5	15.5	34.8
36.6	32.8	12.3	53.0	23.2	------	22.6	------	24.0	14.8	35.5
36.6	36.7	11.4	61.2	24.0	52.5	25.4	39.4	22.1	14.8	34.4
36.6	34.2	11.1	58.2	27.3	------	24.3	------	22.7	15.6	38.8
36.7	34.1	11.1	52.6	25.3	------	23.2	------	23.2	15.5	36.5
36.9	31.7	9.9	59.1	25.0	------	24.9	------	23.0	15.2	37.9
37.1	34.0	12.1	52.9	22.9	------	22.9	------	23.2	16.2	34.8
37.7	34.0	11.0	47.0	23.6	------	23.8	------	22.3	15.6	35.8
38.4	35.4	12.4	50.2	28.6	------	23.2	------	24.0	14.3	36.2
39.2	35.0	11.7	60.5	24.0	------	------	------	23.5	14.5	38.8
39.5	34.4	12.4	53.7	26.8	------	24.5	------	23.5	15.4	37.5
39.8	32.7	11.7	56.3	23.6	------	24.4	------	23.4	14.6	38.9
39.9	34.4	11.2	48.6	24.0	------	23.5	------	22.6	14.8	36.1
40.0	33.5	11.2	52.5	26.0	52.5	25.5	38.0	22.5	15.5	38.0
40.1	34.2	11.8	53.4	23.6	------	23.2	------	23.2	13.7	37.4
40.1	32.4	10.4	50.6	21.9	------	20.6	------	20.2	14.2	32.9
40.1	33.4	11.2	57.1	23.6	------	22.6	------	20.4	14.5	36.2
41.1	33.1	11.1	51.6	25.3	------	22.6	------	22.6	14.8	34.5
41.2	32.3	11.5	58.6	28.2	------	26.5	------	24.0	13.8	37.4
41.9	34.4	11.7	54.0	26.0	------	23.4	------	22.0	14.6	36.8
42.1	31.6	11.1	69.0	25.6	56.5	26.6	48.0	24.0	14.7	38.2
42.2	32.0	10.3	51.7	25.8	------	23.9	------	22.7	15.2	36.5
42.5	32.3	11.0	60.0	------	56.0	21.2	42.2	22.1	14.4	------
42.6	35.2	12.0	58.3	27.0	53.5	25.6	40.5	24.2	18.1	39.4
42.9	33.6	11.7	54.9	25.2	51.3	23.4	40.0	23.1	------	36.8
42.9	34.8	11.7	54.9	25.7	------	24.0	------	22.8	15.2	37.5
43.9	34.4	11.8	54.5	27.2	------	24.2	------	23.0	13.7	36.9
44.2	34.8	11.5	51.5	24.6	------	25.1	------	22.3	14.5	37.8
44.8	33.2	10.8	57.4	25.9	------	23.7	------	20.3	14.7	35.9
44.8	33.2	11.4	53.2	27.0	------	25.5	------	23.2	14.5	37.7
44.9	34.4	11.8	57.0	26.6	53.7	25.4	42.6	23.2	16.4	37.4
44.9	31.7	9.8	56.9	------	53.8	------	------	20.7	13.8	34.7
46.4	31.1	10.4	57.9	25.7	52.1	25.5	42.9	20.5	13.8	34.9
46.6	30.7	10.9	49.6	32.4	------	28.4	------	24.9	13.7	41.6
46.6	31.8	10.5	67.8	22.5	------	22.3	------	20.2	15.2	33.9
48.3	35.6	12.2	57.0	27.4	54.0	26.2	42.3	24.2	15.5	38.7
48.8	34.6	11.5	66.5	30.6	------	27.3	------	22.3	15.2	38.3
49.0	32.9	11.0	52.1	23.3	------	23.4	------	23.1	13.9	36.3
51.0	32.0	10.8	60.8	29.4	55.0	22.6	44.5	26.1	12.2	38.4
51.0	32.4	11.6	55.5	25.8	------	26.9	------	20.8	15.1	35.1
51.5	33.8	11.7	53.8	30.2	------	27.4	------	23.1	15.7	39.2
52.0	31.9	11.0	52.1	28.1	52.3	25.8	40.8	22.1	14.6	36.5
52.0	32.9	11.5	52.9	28.8	------	23.9	------	23.3	14.2	38.1
55.0	33.3	10.7	53.4	27.1	------	24.2	------	22.4	14.0	35.8
55.5	33.2	10.6	60.0	29.0	55.1	25.0	43.0	23.4	15.0	37.5
56.0	31.6	10.7	61.6	31.5	54.6	27.0	41.5	23.4	14.1	38.4
57.0	30.9	11.2	55.2	26.7	55.0	25.1	41.5	20.7	14.7	36.1
57.0	33.0	10.2	55.3	29.6	------	24.8	------	23.2	14.7	37.9
59.0	34.3	10.8	51.9	27.5	------	25.4	------	------	14.1	36.4
59.5	32.5	11.4	75.4	36.4	59.2	30.4	48.7	21.3	14.5	38.8
63.5	30.9	10.1	66.5	33.4	55.0	26.2	45.0	23.5	13.7	40.5
64.5	31.5	11.9	56.6	31.4	54.6	------	41.7	23.6	14.6	40.9

APPENDIX TABLE 2.—*Measurements of selected body proportions for* Trachinotus *spp., expressed as percent of standard length*—Continued

Standard length (mm.)	Percent of standard length									
	Head length	Eye diameter	Body depth	Dorsal fin		Anal fin		Pectoral fin length	Pelvic-fin length	Caudal-fin lobe length
				Lobe length	Base length	Lobe length	Base length			
T. falcatus—Con.										
64.5	30.9	10.2	57.7	28.7	54.8	-----	44.1	20.8	13.8	35.7
66.5	32.2	10.5	56.5	30.6	-----	28.1	-----	23.3	14.1	37.7
74.0	29.6	9.9	66.3	30.2	56.3	29.7	43.6	24.1	12.7	39.5
75.5	28.9	9.5	63.0	34.8	56.9	27.4	45.4	22.6	13.0	37.6
76.0	30.1	9.5	58.4	33.6	53.5	26.4	44.5	20.7	12.4	36.1
84.0	29.8	9.8	67.8	36.7	57.6	29.0	46.5	22.4	12.1	39.4
85.0	31.2	10.0	59.0	35.0	55.5	29.2	43.9	21.9	13.4	36.4
85.0	28.6	9.7	69.4	35.5	54.5	26.8	45.4	22.4	12.2	36.6
85.5	31.8	10.8	65.6	43.0	57.0	33.6	46.6	23.6	13.5	45.6
89.5	29.2	9.4	58.2	35.4	55.9	28.5	45.2	21.7	15.2	39.0
100.0	28.9	9.3	63.0	33.9	55.5	29.1	45.0	21.0	12.1	37.2
102.0	28.6	9.1	64.2	37.8	55.9	28.1	46.6	22.4	13.2	40.7
103.0	29.2	9.5	59.7	35.2	55.5	26.3	44.7	21.0	13.3	34.3
125.5	27.0	8.7	64.1	39.8	56.1	32.0	47.0	21.8	11.9	33.9
127.5	27.8	8.3	68.5	42.7	59.6	33.4	47.5	23.6	-----	42.7
132.0	29.3	9.4	64.4	47.0	56.0	36.8	45.8	24.0	12.3	-----
133.5	30.4	8.7	63.6	44.2	56.5	35.7	45.0	22.6	12.5	44.2
136.5	30.1	8.8	68.0	42.5	57.9	32.2	47.6	21.9	12.5	41.0
154.5	26.9	8.5	63.0	32.4	57.0	33.6	46.3	21.4	11.7	43.4
172.0	25.2	8.3	62.0	-----	58.1	33.7	46.0	20.6	12.0	44.8
174.0	26.8	7.9	63.8	46.0	56.0	37.4	44.2	21.7	10.7	44.3
182.0	25.7	7.5	61.0	44.0	57.8	35.3	45.6	21.0	11.0	42.9
216.5	26.5	7.9	57.3	47.0	55.5	30.0	46.1	21.9	10.5	45.5
T. glaucus:										
7.8	38.8	14.0	35.8	-----	42.0	-----	28.0	-----	9.4	33.4
11.8	41.0	14.3	35.0	-----	42.0	-----	27.4	23.3	18.0	34.5
14.6	36.3	12.9	36.3	22.6	45.2	22.1	29.7	24.4	16.9	35.0
16.6	35.6	12.8	34.4	-----	45.8	22.5	31.3	25.0	17.4	35.5
19.4	34.5	10.9	36.0	-----	43.8	-----	30.4	21.3	14.7	34.5
23.3	34.8	11.2	38.2	24.0	44.6	23.2	30.5	20.1	17.3	34.9
23.9	35.5	10.4	32.2	23.4	45.2	22.6	30.1	23.0	16.8	34.7
24.0	33.8	9.8	35.0	25.4	45.0	23.8	30.8	21.6	17.0	35.0
26.2	32.4	10.4	30.5	24.8	47.3	21.7	32.1	22.5	17.5	35.5
28.9	34.2	9.7	32.2	23.5	44.6	19.4	29.4	19.4	16.5	34.3
35.8	35.3	10.4	36.8	24.6	47.2	22.6	32.1	22.4	19.6	36.0
36.0	33.9	9.2	31.7	25.2	48.3	24.2	31.7	22.7	16.7	35.6
36.5	32.9	9.3	31.0	25.4	46.8	24.0	31.5	22.2	17.0	35.9
39.2	33.0	9.7	31.9	24.5	47.7	24.7	33.7	23.2	17.6	35.2
39.4	33.2	9.7	38.9	23.8	48.2	23.6	32.7	22.1	16.5	35.3
44.8	33.1	9.3	38.2	26.4	46.9	26.7	35.3	21.0	18.3	36.0
44.8	33.7	9.3	33.3	26.6	49.6	25.7	33.7	22.1	16.9	36.6
45.0	32.1	10.0	37.2	26.9	47.1	26.0	33.6	22.7	17.1	36.7

APPENDIX TABLE 2.—*Measurements of selected body proportions for* Trachinotus *spp., expressed as percent of standard length*—Continued

Standard length (mm.)	Percent of standard length									
	Head length	Eye diameter	Body depth	Dorsal fin		Anal fin		Pectoral fin length	Pelvic-fin length	Caudal-fin lobe length
				Lobe length	Base length	Lobe length	Base length			
T. glaucus—Con.										
46.5	32.1	9.0	34.2	27.6	46.5	24.8	33.3	22.4	16.5	35.7
47.1	30.8	9.4	38.0	25.9	49.0	25.7	32.1	23.6	-----	36.3
47.2	31.8	9.0	36.4	25.3	48.7	23.3	33.7	22.0	16.5	35.0
47.8	32.2	9.6	36.4	25.6	47.1	25.1	32.8	22.0	16.9	35.4
48.2	32.2	9.1	39.2	29.5	49.4	26.0	33.4	21.6	16.8	35.4
48.2	32.0	8.8	36.5	26.2	49.4	27.4	32.2	22.4	16.3	35.3
48.5	32.4	9.0	36.1	23.5	48.7	21.9	34.4	22.9	17.7	37.0
50.5	34.0	9.1	35.1	27.0	48.5	23.6	35.0	21.0	16.1	35.6
52.0	33.5	9.1	38.1	25.4	49.4	24.2	36.5	23.3	17.3	39.0
61.0	33.3	8.9	40.3	25.6	49.0	23.3	35.6	22.0	17.1	37.1
63.0	31.1	8.1	41.3	26.5	50.5	27.0	35.9	22.2	17.5	-----
65.0	31.4	8.5	41.4	28.0	51.8	26.5	36.9	22.9	15.7	36.4
68.5	32.3	8.6	42.2	30.8	51.1	27.9	36.9	22.4	16.5	-----
70.0	32.3	8.7	41.3	27.2	49.4	25.8	35.9	20.6	16.3	37.0
71.5	29.5	8.0	42.0	29.5	49.7	29.5	37.8	21.3	18.4	38.2
72.0	30.7	8.5	40.0	29.9	49.6	28.4	35.4	20.7	15.6	38.0
75.0	31.0	8.9	41.8	33.2	50.8	32.4	36.4	22.3	16.4	38.7
76.5	30.6	8.8	39.9	31.9	50.3	29.7	37.1	21.8	14.8	39.8
80.0	31.0	8.0	40.5	34.2	50.0	30.0	38.3	21.3	15.7	40.2
80.0	29.6	8.4	39.4	31.4	50.5	27.0	36.6	20.4	15.9	36.5
81.0	33.4	9.9	39.5	33.5	48.6	30.5	34.3	22.5	15.8	42.8
86.0	29.4	8.7	41.2	32.4	50.5	27.2	38.6	21.4	17.2	38.0
86.5	30.6	8.4	44.6	-----	51.2	30.3	38.6	22.3	16.2	39.7
88.0	28.9	8.1	39.7	27.8	49.8	27.0	38.4	20.9	16.5	37.2
89.0	27.2	7.6	42.0	33.6	51.9	29.9	39.2	22.5	16.9	39.5
94.5	32.3	9.4	45.5	-----	50.3	31.1	34.6	22.8	15.1	43.4
94.5	32.0	8.9	42.8	-----	48.7	30.4	37.6	22.1	14.5	41.0
96.0	32.7	9.2	42.1	41.8	50.8	31.3	37.0	22.2	14.9	-----
97.5	30.7	8.7	43.4	47.5	50.2	38.4	36.4	22.6	15.5	43.8
99.0	30.1	9.5	42.3	-----	49.4	30.4	36.2	22.6	15.1	41.9
101.0	31.2	8.8	43.9	35.7	50.5	29.1	36.2	-----	14.8	-----
102.0	30.5	8.0	44.7	34.4	50.5	28.9	37.1	21.6	14.7	40.1
110.0	30.7	8.6	45.0	-----	51.8	40.5	37.0	21.4	14.6	42.8
116.5	28.5	8.4	47.2	50.6	53.2	45.5	40.4	21.7	14.2	44.6
124.0	28.4	8.3	48.4	64.5	53.2	50.4	40.3	21.7	14.8	47.3
128.0	27.9	8.7	46.9	-----	51.2	-----	38.5	21.3	14.5	-----
139.0	28.5	7.3	50.0	50.8	53.6	45.0	39.9	21.2	12.1	42.8
141.5	26.2	7.3	46.6	53.0	53.7	53.0	40.6	21.8	14.3	46.0
211.0	26.1	7.4	53.3	72.0	55.0	67.0	43.4	21.2	13.0	-----

EFFECT OF CERTAIN ELECTRICAL PARAMETERS AND WATER RESISTIVITIES ON MORTALITY OF FINGERLING SILVER SALMON

By JOHN R. PUGH, *Fishery Research Biologist*

BUREAU OF COMMERCIAL FISHERIES

Biologists have been searching for many years for an effective method of diverting salmon fingerlings from hazardous areas, such as turbine intakes, spillways, and high-velocity channels. In their search, they have explored the possibilities of physical barriers, sound-producing instruments, air bubbles, lights, controlled water velocities, chemicals, and electricity.

To further this research, the electrical guiding project of the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash., conducts extensive studies to determine the effectiveness of guiding or diverting salmon fingerlings with electricity. We have progressed from small-scale laboratory studies to field sites on small streams [1] and, currently, to a large-scale field investigation.[2]

With each of these field studies there has been associated laboratory work to determine whether the electrical conditions to be tested are harmful to the fish. Collins, Volz, and Trefethen (1954) found that mortality increased with an increase in total voltage, pulse frequency, duration of exposure, water temperature, or with combinations of these factors. Raymond (1956) noted a slight loss in fish in tests with duty cycles of 0.10 or greater. Maxfield [3] found, over the range of electrical conditions which he tested, that the electric shock did not affect the future reproductive ability of young rainbow trout exposed as yearling fish. Trefethen (1955) and Newman (1959b) conducted laboratory investigations in guiding salmon fingerlings with electricity, but made little or no mention of mortality; however, personal interviews with each investigator revealed that very few mortalities occurred in either experiment.

The potential application of electrical guiding techniques depends on the degree of safety, as well as efficiency, with which electrical fields guide or divert fish. Although observations indicate that the number of injuries and mortalities caused by electrical fields is negligible, the question of mortality invariably arises with each new experimental method of diverting fish with electricity.

The objective of this study was to determine, under controlled laboratory conditions, the immediate and delayed effects of certain electrical parameters and water resistivities on the mortality of fingerling silver salmon (*Oncorhynchus kisutch*).

Rea E. Duncan and Donald D. Worlund assisted in the planning of the experimental design and in making the statistical analyses, and Charles C. Gillaspie was responsible for the operation and maintenance of the electronic equipment.

METHOD AND MATERIALS

Experimental design

The experiment was conducted in Latin square sequence using water resistivity, wiring pattern, pulse shape, voltage, and frequency as variables (see table 1). Throughout the experiment the pulse duration was 8.3 milliseconds, the water depth 1 foot, and the average water velocity 1 foot per second. Some of these experimental conditions were similar to conditions tested in earlier research. This similarity enabled us to correlate the results of this experiment with our previous studies. Other conditions were more rigorous in an attempt to establish the maximum level of electrical intensity that could be used at future installations without causing mortalities among the migrating fish.

NOTE.—Approved for publication, June 21, 1961. Fishery Bulletin 208.

[1] Hunter, Charles J. Manuscript in preparation. Experimental guiding of salmonids by electricity. Bureau of Commerical Fisheries Biological Laboratory, Seattle, Wash.

[2] Mason, James E., and Rea E. Duncan. Manuscript in preparation. Development and appraisal of methods of diverting fingerling salmon with electricity at Lake Tapps. Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash.

[3] Maxfield, Oalen H. Manuscript in preparation. Effect of electricity on reproductive ability of rainbow trout. Bureau of Commerical Fisheries Biological Laboratory, Seattle, Wash.

TABLE 1.—*Latin square experimental design*

[The rows are comprised of water resistivities, the columns of wiring patterns and pulse shapes, and the treatments of voltages and frequencies]

	I Half sine-wave	II Square-wave	I Square-wave	II Half sine-wave
5,000 ohm cm	165v.–30 p.p.s	250v.–30 p.p.s	250v.–15 p.p.s	165v.–15 p.p.s.[1]
15,000 ohm cm	250v.–30 p.p.s	165v.–30 p.p.s	165v.–15 p.p.s	250v.–15 p.p.s.
1,000 ohm cm	165v.–15 p.p.s	250v.–15 p.p.s	250v.–30 p.p.s	165v.–30 p.p.s.
10,000 ohm cm	250v.–15 p.p.s	165v.–15 p.p.s	165v.–30 p.p.s	250v.–30 p.p.s.

[1] Pulse per second.

As shown in table 1, a total of 16 tests were conducted with the array energized. In addition, four groups of fish were tested with the power off to serve as controls. Each control group was tested in one of the water resistivity conditions used during the power-on tests. Each group, test or control, consisted of approximately 100 silver salmon fingerlings.

Prior to testing, each group of fish was tattooed with a distinctive mark. The fish were then exposed to electric shock in an experimental tank and, after examination for immediate mortalities, they were transferred to an outdoor holding tank where they were held 30 days for observation. The tattoo marks provided a means of identifying each group of fish during the 30-day holding period. Observations were made daily and a record of mortalities was maintained.

Test fish

The test fish were age-group 0 silver salmon (*O. kisutch*) obtained from the national hatchery at Quilcene, Washington. They were transported to the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash., in an aerated tank and held in outdoor holding tanks prior to testing.

The fish ranged in size from 55 to 98 mm., measured from the tip of the snout to the posterior end of the vertebral column (standard length measurement illustrated by Schultz, 1948). The average standard length was 85 mm.

Laboratory facilities

The experiment was conducted in the fall of 1959 in the main experimental tank of the fish-behavior laboratory described by Newman (1959a). This tank is 20 feet wide, 58 feet 6 inches long, and 5 feet deep. It was divided lengthwise by installing a partition constructed of ¾-inch plywood, creating a channel 10 feet 2 inches wide (fig. 1). Installation of this partition produced the desired conditions (depth of water, 1 foot; average water velocity, 1 foot/second) without altering any of the existing laboratory facilities.

The floor and walls of the experimental channel were coated with asphalt and insulating paint to minimize electrical grounding. Horizontal baffles, designed to produce a uniform flow of water, were installed in the headbox (fig. 2). Both ends of the channel were screened with ¼-inch hardware cloth to confine the fish to the test area.

A release box (fig. 2), 4 feet by 2 feet 10 inches by 2 feet with a removable gate, was placed in the channel approximately 8 feet downstream from the headbox. A block-and-tackle assembly enabled us to remove the box from the water after release of the test fish. A second box with the same design and dimensions, but fitted with lead-in nets, was placed at the downstream end of the channel (fig. 3). This second box was used in the recovery of the fingerlings after they had passed through the test area.

Two troughs, each 66½ by 9½ by 8½ inches, were set up in an area adjacent to the experimental tank (fig. 4). One trough was placed on a rack 4 inches higher than the other and served as a gravity-flow reservoir for the lower trough and a holding area for the fish prior to tattooing. The lower trough served as a table for the tattooing machine and as a holding area for the test fish after they had been tattooed. Water was supplied to the upper trough at a rate of one-half gallon per minute by means of a submersible pump placed in the headbox of the main experimental tank. A standpipe overflow returned the water from the lower trough through a flexible hose to the experimental tank headbox. This system maintained a constant flow of water through the troughs and a stable water level in the experimental tank.

Electrical equipment and test conditions

Array.—The electrode array consisted of a 10- by 5½-foot wooden framework with cross mem-

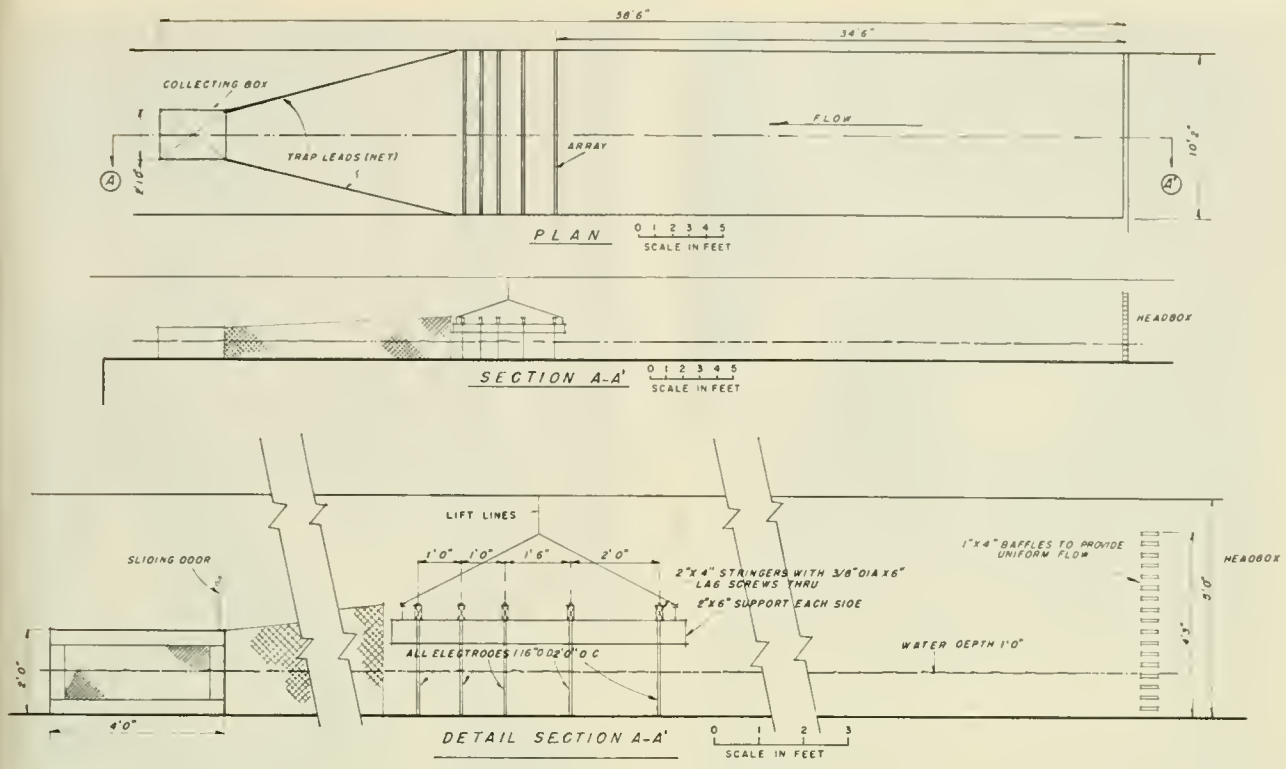

FIGURE 1.—Plan and cross-sectional view of experimental channel.

bers to support the electrodes, their connecting wires, and the electrical-pulse supply cables from the sequential switching equipment (fig. 5). The array was suspended so that the bottoms of the electrodes were ½ inch from the bottom of the tank. The electrodes were 2½-foot lengths of galvanized electrical conduit with an outside diameter of 1.163 inches. They were arranged in five staggered rows with 2-foot spaces between the electrodes in each row. The upstream row of electrodes was designated row A and the downstream row, row E. The spacing was 2 feet between rows A and B, 1½ feet between rows B and C, 1 foot between rows C and D, and 1 foot between rows D and E (fig. 6). The applied voltage to all electrodes was the same; hence, the decreasing distance between electrode rows created an area of higher voltage gradient on the downstream side of the array.

Water resistivity.—Four levels of water resistivity, 1,000, 5,000, 10,000, and 15,000 ohm centimeters, were tested.

Pulse shape.—The tests included two variations of pulse shape: square-wave and half sine-wave (fig. 7).

Pulse amplitude.—Two levels of applied peak voltage were tested: 165 and 250 volts.

Pulse duration.—The pulse duration for both the square-wave and the half sine-wave pulses was 8.3 milliseconds.

Sequential switching equipment.—The electronic equipment that supplied the square-wave pulses consisted of a pulse generator that sequentially switched the output of a direct current generator to various groups of electrodes. The d.c. generator was powered by commercially available 60-cycle alternating current. Figure 8 is a block diagram of this equipment. A detailed description and schematic diagrams of the switching equipment are being prepared and will be published at a later date.[4]

The equipment that supplied the half sine-wave pulses was essentially the same as that which supplied the square-wave pulses, except that the d.c. generator, the overload protector, and the exciter were replaced by 60-cycle alternating

[4] Volz, Charles D., and H. P. Dale. Manuscript in preparation. A high-power pulse generator for electrical fish-guiding research. Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash.

FIGURE 2.—Release box with sliding gate closed. Horizontal baffles and headbox are shown in background.

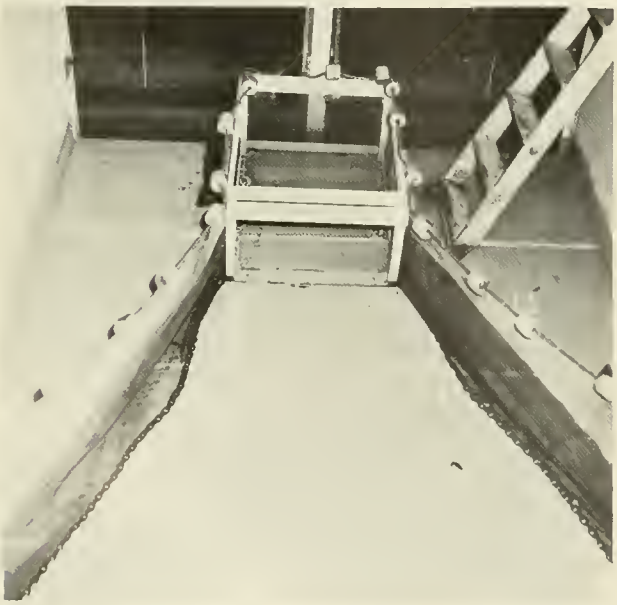

FIGURE 3.—Recovery box with sliding gate removed. Lead-in nets are shown in foreground; downstream screens in the background.

FIGURE 4.—Tattooing facilities.

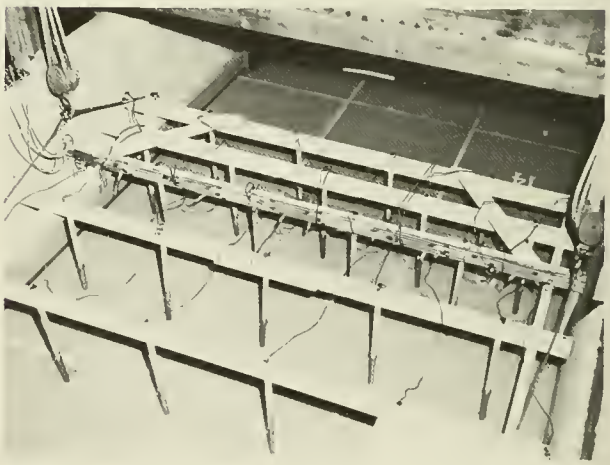

FIGURE 5.—Staggered electrode array used in this experiment.

current, supplied by a line transformer. Figure 9 is a block diagram of this modified equipment.

Wiring patterns.—The two wiring patterns tested are illustrated in figure 10. With each of these patterns, the electrodes were energized by the sequential switching equipment in such a

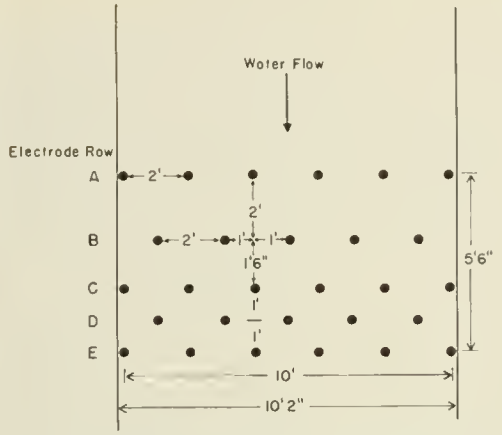

FIGURE 6.—Staggered electrode array with spacing as indicated. (Heavy dots represent the electrodes.)

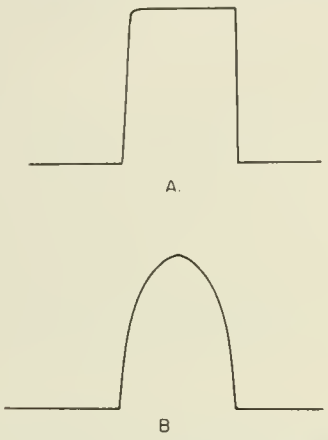

FIGURE 7.—Square-wave (A) and half sine-wave (B) pulses.

manner that five electrical fields were produced. These fields will be discussed later in the text.

Pulse frequency.—Frequencies of 15 and 30 pulses per second were tested. Since both wiring patterns produced five electrical fields, each field was pulsed either three or six times per second, depending on the frequency being used, i.e., frequency divided by number of electrical fields.

Sequential pulsing—When the array was wired according to wiring pattern I (fig. 10) and energized with square-wave pulses, the polarity of the

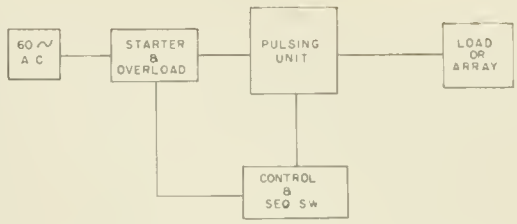

FIGURE 9.—Block diagram of sequential switching equipment used to supply half sine-wave pulses,

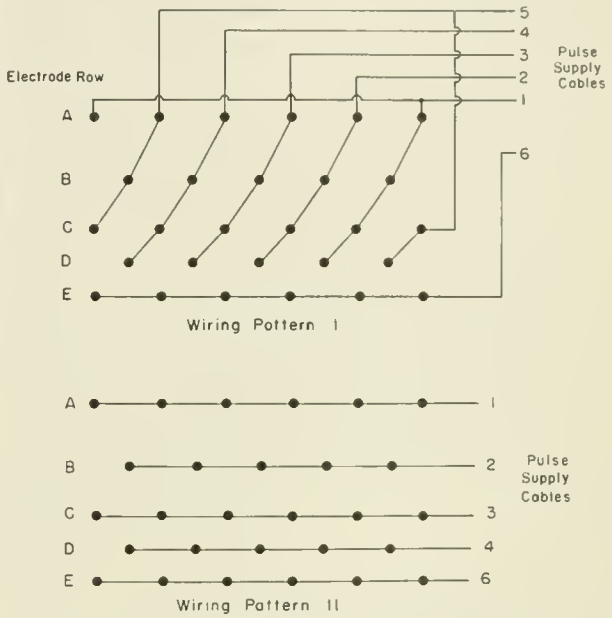

FIGURE 10.—Wiring patterns used in the experiment. (Heavy dots represent the electrodes.)

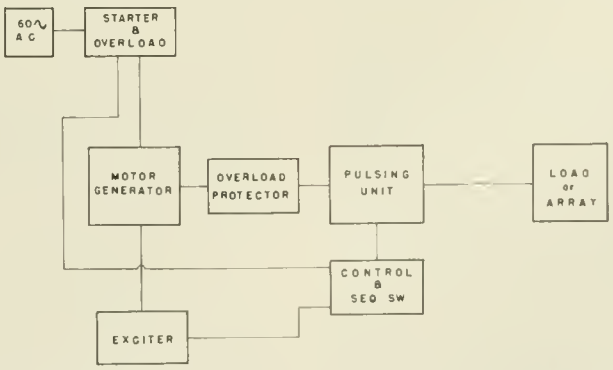

FIGURE 8.—Block diagram of sequential switching equipment used to supply square-wave pulses.

electrodes was alternated with each successive pulse and a sequence of pulses, moving from left to right looking downstream, was established. Table 2 shows this pulsing sequence.

When the first pulse was delivered, the electrodes connected to pulse supply-cable 1 became positive and the electrodes connected to pulse supply-cable 6 (row E) became negative. On the second pulse, the electrodes connected to pulse supply-cable 2 became negative and the electrodes in row E became positive. This sequence of pulses and alternating polarity continued through pulse supply-cables 3, 4, and 5 to complete the cycle. Then, on the first pulse of the second cycle, the electrodes connected to pulse supply-cable 1 became negative and the electrodes in row E became positive. On the second pulse of the second cycle the electrodes connected to pulse supply-cable 2 became positive and the electrodes in row E became negative. Again, this succession of pulses and alternating polarity continued through pulse supply-cables 3, 4, and 5 to complete the second cycle. In the third cycle, the electrodes were energized and the polarity alternated as they were during the first cycle. This process was an automatic function of the sequential switching equipment.

TABLE 2.—*Pulsing sequence and polarity changes when the electrodes were wired according to wiring pattern I and energized with square-wave pulses*

Pulse supply-cable	Pulsing sequence and polarity changes					
	Pulse 1	Pulse 2	Pulse 3	Pulse 4	Pulse 5	Pulse 1 (second cycle)
1	(+)	0	0	0	0	(−)
2	0	(−)	0	0	0	0
3	0	0	(+)	0	0	0
4	0	0	0	(−)	0	0
5	0	0	0	0	(+)	0
6 (row E)	(−)	(+)	(−)	(+)	(−)	(+)

Because of technical limitations of the existing sequential switching equipment, polarity of the electrodes was not alternated when the array was wired according to wiring pattern I and energized with half sine-wave pulses. The sequence for this switching operation is shown in table 3.

The first pulse from the switching equipment energized only the electrodes connected to pulse supply-cable 1, making them positive, and the electrodes in row E, making them negative. The second pulse energized the electrodes connected to pulse supply-cable 2, making them positive and again the electrodes in row E became negative. This sequence continued through pulse supply-cables 3, 4, and 5, until five successive pulses had been delivered. The electrodes in row E were of negative polarity with each pulse. When the fifth pulse had been delivered, the cycle was completed and the sequence was automatically repeated.

When the array was wired according to wiring pattern II, the pulsing sequence and polarity changes were the same for both the square-wave and the half sine-wave pulses. Table 4 illustrates the pulsing sequence for wiring pattern II.

The first pulse energized rows D and E, making row D positive and row E negative. On the second pulse, row D became negative and row C positive. On the third pulse, row C was negative and row B positive. On the fourth pulse, row B became negative and row A positive; and on the fifth pulse, row A became negative and row E positive. When this sequence was completed, the cycle was automatically repeated.

Voltage gradients.—The electrical fields created by the two wiring patterns were determined by analog gradient plotting and are shown in figures 11 and 12. The plotting interval is 10 percent of

TABLE 3.—*Pulsing sequence when electrodes were wired according to wiring pattern I and energized with half sine-wave pulses*

[Polarity not alternated with this configuration]

Pulse supply-cable	Pulsing sequence					
	Pulse 1	Pulse 2	Pulse 3	Pulse 4	Pulse 5	Pulse 1 (second cycle)
1	(+)	0	0	0	0	(+)
2	0	(+)	0	0	0	0
3	0	0	(+)	0	0	0
4	0	0	0	(+)	0	0
5	0	0	0	0	(+)	0
6 (row E)	(−)	(−)	(−)	(−)	(−)	(−)

TABLE 4.—*Pulsing sequence and polarity changes when electrodes were wired according to wiring pattern II and energized with either square-wave or half sine-wave pulses*

Electrode row	Pulsing sequence and polarity changes					
	Pulse 1	Pulse 2	Pulse 3	Pulse 4	Pulse 5	Pulse 1 (second cycle)
A	0	0	0	(+)	(−)	0
B	0	0	(+)	(−)	0	0
C	0	(+)	(−)	0	0	0
D	(+)	(−)	0	0	0	(+)
E	(−)	0	0	0	(+)	(−)

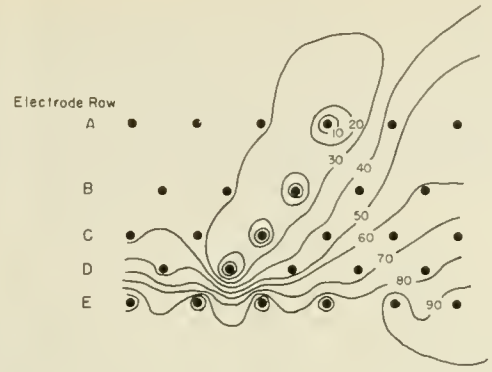

FIGURE 11.—Electrical field created on the third pulse of the cycle when the array was wired according to wiring pattern I. (Lines connect points of equal potential; numbers show percentage of the applied voltage. Heavy dots represent the electrodes.)

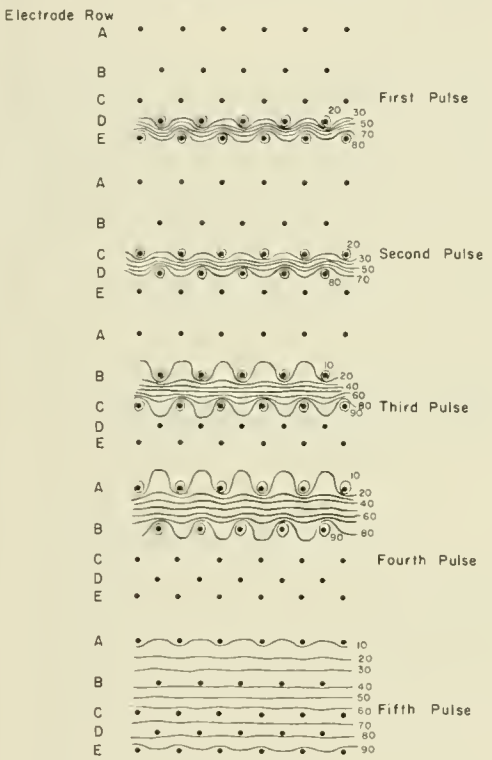

FIGURE 12.—Electrical fields created during one complete cycle when the array was wired according to wiring pattern II. (Lines connect points of equal potential; numbers show percentage of the applied voltage. Heavy dots represent the electrodes.)

the applied voltage. Figure 11 shows the electrical field produced when the array was wired according to wiring pattern I. Only one pulse of the five-pulse cycle is illustrated, but it is representative of the electrical fields produced with each pulse, since the wiring pattern was uniform with respect to electrode spacing.

Wiring pattern II was not uniform with respect to electrode spacing, and therefore each pulse created a slightly different electrical field. The electrical fields established when the array was wired in this pattern are shown in figure 12.

Experimental procedure

Before the start of each test the electrodes were connected to create the desired wiring pattern. The sequential switching equipment was turned on and, with a calibrated oscilloscope as a monitor, was adjusted to supply the correct pulse parameters. When the switching equipment was functioning properly, it was turned off until the test fish had been placed in the release box.

Water resistivity was measured by means of a commercial conductivity bridge and regulated to the desired level by adding rock salt or by draining the tank and adding fresh water. Facilities were not available to control water temperature, and it varied from 63° F. at the beginning of the experiment (September 16, 1959) to 59.5° F. at the end of the experiment (October 14, 1959). Temperature readings were taken with a standard mercury thermometer.

Before each test, approximately 100 fish were transferred from an outdoor holding tank to the rectangular troughs in the fish-behavior laboratory for marking. Then, in groups of 10, the fish were anesthetized in a solution of tricaine methanesulfonate (M.S. 222) at a concentration of 1:20,000, and tattooed with mineral pigments. When approximately 100 fish had been marked, and all had recovered from the anesthetic, they were placed in the release box in the test channel. In order to observe and remove mortalities due to handling, the fish were held in the release box from 10-15 minutes before the tests were initiated.

The array was then energized with the preset electrical conditions and a pump was started to provide a flow of water through the channel. Next, the sliding gate on the release box was raised, and the fish were released. When all of the fingerlings had left it, the box was hoisted clear of the water by means of the block-and-tackle assembly.

To ensure that all of the fish were exposed to the electrical energy, they were forced to swim through the array by crowding them with a seine. They were then captured in the recovery

box below the electrical array, counted, and examined for mortalities or any sign of visible injury. The average time required to conduct each test, from the time the fish were released until they were recaptured, was 25 minutes.

After all of the fish had been examined and the data recorded, they were transferred to an outdoor holding tank where they were held 30 days for observation. The dead fish were picked out daily and carefully examined for marks or bruises. At the termination of the experiment, the live fish were also examined for any signs of visible injury and the results were tabulated.

After every fourth power-on test, but before the water resistivity was changed for the next series of tests, approximately 100 control fish were tattooed and released into the experimental tank. The control fish were handled in exactly the same manner as the test fish, except that the array was not energized while they were in the experimental tank.

The statistical analysis that follows is based on a comparison of the differences in mortality in the fish tested under the various electrical conditions and also on a comparison of the mortality of the test fish with that of the control fish. These comparisons were made for the differences that occurred during the first 24 hours following the testing and also for the differences that occurred during the second to thirtieth day after testing.

RESULTS AND DISCUSSION

The experimental results are summarized in table 5, and include the number and percentage of fish dead after one day and the cumulative mortalities, by number and percentage, from the second to the thirtieth day. The data from table 5 were transformed from percentages to arc sin $\sqrt{\text{percentage}}$ and the entire analysis was made with the transformed data.

Immediate effect

Analysis of variance (table 6) to determine the immediate effect (during the first day) of the variables tested reveals that at the 5-percent significance level a higher mortality resulted from the square-wave pulses than from the half sine-wave pulses, and that a higher mortality resulted from

TABLE 5.—*Immediate (1st day) and delayed (2d to 30th day) mortalities, by number and percentage, of the test fish and control fish*

Test No.	Test conditions [1]	Number of fish released	Died 1st day		Died 2d-30th day	
			Number	Percent	Number	Percent
	5,000 ohm cm.					
Test fish:						
1	I, HSW, 165 v.–30 p.p.s.	96	8	8.3	17	19.3
2	II, SW, 250 v.–30 p.p.s.	96	17	17.7	17	21.5
3	I, SW, 250 v.–15 p.p.s.	96	5	5.2	15	16.5
4	II, HSW, 165 v.–15 p.p.s.	99	1	1.0	13	13.3
Control: 1-C		100	2	2.0	15	15.3
	15,000 ohm cm.					
Test fish:						
5	I, HSW, 250 v.–30 p.p.s.	99	4	4.0	16	16.8
6	II, SW, 165 v.–30 p.p.s.	95	4	4.2	5	5.5
7	I, SW, 165 v.–15 p.p.s.	98	6	6.1	18	19.6
8	II, HSW, 250 v.–15 p.p.s.	99	3	3.0	3	3.1
Control: 2-C		99	2	2.0	9	9.3
	1,000 ohm cm.					
Test fish:						
9	I, HSW, 165 v.–15 p.p.s.	98	4	4.1	9	9.6
10	II, SW, 250 v.–15 p.p.s.	99	12	12.1	25	28.7
11	I, SW, 250 v.–30 p.p.s.	98	18	18.4	8	10.0
12	II, HSW, 165 v.–30 p.p.s.	98	6	6.1	9	9.8
Control: 3-C		100	4	4.0	5	5.2
	10,000 ohm cm.					
Test fish:						
13	I, HSW, 250 v.–15 p.p.s.	108	1	0.9	9	8.4
14	II, SW, 165 v.–15 p.p.s.	108	2	1.9	11	10.4
15	I, SW, 165 v.–30 p.p.s.	99	7	7.1	2	2.2
16	II, HSW, 250 v.—30 p.p.s.	108	6	5.6	10	9.8
Control: 4-C		104	2	1.9	7	6.9

[1] Explanation of test condition symbols:
I—Wiring pattern I.
II—Wiring pattern II.
SW—Square-wave pulses.
HSW—Half sine-wave pulses.
p.p.s.—Pulses per second.

the high frequency (30 pulses per second total or 6 p.p.s. per field) than from the low frequency (15 p.p.s. total or 3 p.p.s. per field).

TABLE 6.—*Analysis of variance of the immediate effect (1st day) of water resistivity (rows), wiring pattern and pulse shape (columns), and voltage and frequency (treatments), on mortality of fingerling silver salmon*

Source of variation	Sum of squares	Degrees of freedom	Mean square	*F*
Water resistivity	129.9289	3	43.3096	3.23
Wiring pattern and pulse shape	123.9093	3		
Wiring pattern	1.5813	1	1.5813	0.118
Pulse shape	122.1578	1	122.1578	*9.109
Interaction	0.1702	1	0.1702	0.013
Voltage and frequency	175.6544	3		
Voltage	43.9238	1	43.9238	3.275
Frequency	127.8596	1	127.8596	*9.534
Interaction	3.8710	1	3.8710	0.289
Residual	80.4669	6	13.4112	
Total	509.9595	15		

*Significant at 5-percent level.

As previously mentioned, polarity of the electrodes was not alternated when the array was wired according to wiring pattern I and energized with half sine-wave pulses. The polarity of the electrodes was alternated, however, when the array was wired according to wiring pattern I and energized with square-wave pulses. Therefore, the difference in mortality which in table 6 is attributed to the difference between pulse shapes could, in wiring pattern I, be due to the effect of alternating polarity, or to a combination of alternating polarity and the difference between pulse shapes, rather than to the difference between pulse shapes alone.

If the difference in mortality rates was due to alternating polarity, either alone or in combination with pulse shape, the analysis would be expected to show a significantly higher mortality resulting from wiring pattern II than from wiring pattern I, since polarity of the electrodes was alternated for both pulse shapes when the array was wired according to pattern II. Also, the analysis would be expected to show significance for the interaction of wiring patterns and pulse shapes. In both of these analyses, however, the differences are not significant. Therefore, we have concluded that the difference in mortality was due to the difference between pulse shapes and not to the effect of alternating polarity. Figure 13 is a comparison of the two pulse shapes and substantiates this conclusion. The figure shows that the total electrical energy of a square-wave

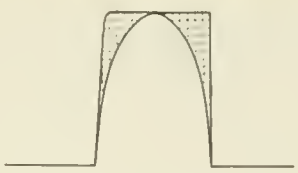

FIGURE 13.—Comparison of square-wave and half sine-wave pulses. Shaded area indicates additional amount of electrical energy available to the fish with each square-wave pulse.

pulse is approximately 30 percent greater than that of a half sine-wave pulse at any constant value of voltage, frequency, and duration.

Total electrical energy is directly proportional to frequency, providing pulse shape, voltage, and pulse duration remain constant. Therefore, the fish subjected to the high frequency experienced twice as much electrical energy as the fish subjected to the low frequency. This difference in total electrical energy explains the higher mortality that resulted from the high frequency.

Although no significant differences in mortality resulted from the differences between the variations of water resistivity, wiring pattern, and voltage, certain indications are apparent from the table of means (table 7) and are summarized as follows:

Water resistivity.—Mortalities that resulted from the four levels of water resistivity were combined into two groups: those resulting from the low levels (1,000 and 5,000 ohm cm.) form one group and those resulting from the high levels (10,000 and 15,000 ohm cm.) form the other. Under the conditions tested, it is apparent that the low levels of water resistivity resulted in a higher percentage of losses than the high levels. The analysis of variance shown in table 8 reveals that this difference is significant at the 5-percent level.

Wiring pattern.—The difference in mortality that can be attributed to the difference between wiring patterns I and II is only 0.5 percent.

Voltage.—High voltage (250 volts) appears to have resulted in a higher percentage of losses than low voltage (165 volts).

Analysis of variance shows that significant differences in mortality resulted from the differences between the variations of pulse shape, frequency, and water resistivity (when the mortalities resulting from the four levels of water resistivity were combined into a high and a low group and the variance test was between groups). However, it

TABLE 7.—*Immediate (first day) mean percentage mortality resulting from each of the test conditions*

[Table of means]

Test conditions	Arc sin √percentage	Percent	Group percent
Water resistivity:			
1,000 ohm cm.	17.94	9.5	8.1
5,000 ohm cm.	15.14	6.8	
10,000 ohm cm.	10.62	3.4	3.8
15,000 ohm cm.	11.91	4.3	
Wiring pattern:			
I	14.22	6.0	
II	13.59	5.5	
Pulse shape:			
Square wave	16.67	8.2	
Half sine wave	11.14	3.7	
Voltage:			
Low (165 v.)	12.24	4.5	
High (250 v.)	15.58	7.2	
Frequency:			
Low (15 p.p.s.)	11.08	3.7	
High (30 p.p.s.)	16.73	8.3	

TABLE 8.—*Analysis of variance of the immediate effect (1st day) of low (1,000 and 5,000 ohm cm.) and high (10,000 and 15,000 ohm cm.) levels of water resistivity on the mortality of fingerling silver salmon*

Source of variation	Sum of squares	Degrees of freedom	Mean square	F
Water resistivity [1]	129.9289	3	43.3096	3.23
Low vs. high	110.9336	1	110.9336	*8.2717
Remainder	18.9953	2	9.4976	0.708
Residual	80.4669	6	13.4112	

[1] See table 6.
* Significant at 5-percent level.

does not show whether the least-harmful variations of these test conditions caused a significant number of mortalities in the test fish compared with that in the control fish. Therefore, a chi-square analysis was conducted to determine whether a difference in mortality existed between the test fish and the control fish.

In this analysis, the mortalities resulting from the low and high levels of water resistivity and each variation of pulse shape and frequency were grouped into eight combinations. Each combination included the mortalities resulting from one variation of each of these three variables. The total percentage mortality of each combination was then compared with the total percentage mortality of the controls. The results of this analysis are shown in table 9.

Table 9 reveals that the least-harmful test variations (high water resistivity, half sine-wave pulses, and low frequency) did not cause a significantly higher mortality of test fish than of the control fish. The table also shows that the test variations caused a high mortality only when two or more of the harmful variations were combined.

TABLE 9.—*Chi-square comparison of the immediate (1st day) mortality of the test fish with that of the control fish*

Comparison [1]	Sample size	No. of deaths	Percent	Degrees of freedom	X^2
Control	403	10	2.48		
LR, LF, HSW	197	5	2.54	1	0.00
Control	403	10	2.48		
LR, HF, HSW	194	14	7.22	1	*7.62
Control	403	10	2.48		
LR, LF, SW	195	17	8.71	1	*11.85
Control	403	10	2.48		
LR, HF, SW	194	35	18.04	1	*45.60
Control	403	10	2.48		
HR, LF, HSW	207	4	1.93	1	0.205
Control	403	10	2.48		
HR, HF, HSW	207	10	4.83	1	2.437
Control	403	10	2.48		
HR, LF, SW	206	8	3.88	1	0.958
Control	403	10	2.48		
HR, HF, SW	194	11	5.67	1	*3.97

[1] Explanation of symbols:
LR—Low levels of water resistivity (1,000 and 5,000 ohm cm.).
HR—High levels of water resistivity (10,000 and 15,000 ohm cm.).
LF—Low frequency (15 p.p.s.).
HF—High frequency (30 p.p.s.).
HSW—Half sine-wave pulses.
SW—Square-wave pulses.
* Significant at 5-percent level.

This analysis is based on the assumption that the variations of wiring pattern and voltage did not cause a significant number of deaths among the test fish when compared with the control fish. However, since voltage and wiring pattern were integral parameters of the experiment, they were factors in the results of the analysis. Therefore, they would have caused the entire analysis to show significance if the variations of either had caused a significant number of mortalities in the test fish as compared with that in the control fish.

The analysis is also based on the assumption that no differences in mortality existed among the four groups of control fish. To test this assumption, another chi-square analysis was made, and it showed that the differences in mortality among control groups were not significant at the 5-percent level. The chi-square value for this test was 1.273 with 3 degrees of freedom.

Delayed effect

Analysis of variance to determine the delayed effect (second to thirtieth day) reveals that at the 5-percent significance level there were no differences in mortality that could be attributed to the differences between the test variations (table 10). Again, however, certain indications are apparent from a table of means (table 11) and are summarized as follows:

General.—With the exception of frequency, the variations of the test conditions resulted in approximately the same differences in mortality

TABLE 10.—*Analysis of variance of the delayed effect (2d to 30th day) of water resistivity (rows), wiring pattern and pulse shape (columns), and voltage and frequency (treatments), upon the mortality of fingerling silver salmon*

Source of variation	Sum of squares	Degrees of freedom	Mean square	*F*
Water resistivity	188.5606	3	62.8535	1.377
Wiring pattern and pulse shape	82.4236	3		
Wiring pattern	0.2450	1	0.2450	0.005
Pulse shape	16.8921	1	16.8921	0.357
Interaction	65.2864	1	65.2864	1.430
Voltage and frequency	71.8659	3		
Voltage	27.4052	1	27.4052	0.600
Frequency	10.5300	1	10.5300	0.231
Interaction	33.9306	1	33.9306	0.743
Residual	273.9149	6	45.6525	
Total	616.7650	15		

after 30 days as they did after 1 day. These differences, however, were not significant because of an increase in residual error.

Pulse frequency.—The difference in mortality which resulted from the difference between levels of frequency actually reversed in sign. This is presumably another indication of the increase in residual error.

Water resistivity.—Mortalities which resulted from each of the four levels of water resistivity were combined in a low and a high group as they were for the analysis of the immediate effect. Analysis of variance (table 12) reveals no significant difference in mortality between the two groups after 30 days.

TABLE 11.—*Cumulative mean percentage mortality (2d to 30th day), resulting from each of the test conditions*

[Table of means]

Test conditions	Arc sin $\sqrt{\text{percentage}}$	Percent	Group percent
Water resistivity:			
1,000 ohm cm	21.78	13.8	15.6
5,000 ohm cm	24.76	17.5	
10,000 ohm cm	15.61	7.2	8.6
15,000 ohm cm	18.54	10.1	
Wiring pattern:			
I	20.30	12.0	
II	20.05	11.8	
Pulse shape:			
Square wave	21.20	13.1	
Half sine wave	19.15	10.8	
Voltage:			
Low (165 v.)	18.86	10.4	
High (250 v.)	21.48	13.4	
Frequency:			
Low (15 p.p.s.)	20.98	12.8	
High (30 p.p.s.)	19.36	11.0	

Chi-square analysis showed that after the 30-day holding period there was no longer a significant difference in mortality between the control fish and the test fish. The chi-square value of this comparison was 3.476, with 1 degree of freedom. In this analysis the total percentage mortality of the control fish, measured from the second through the thirtieth day, was compared with the corresponding mortality of the test fish. A preliminary chi-square analysis showed no significant differences in mortality between the control groups ($X^2=6.8737$, with 3 degrees of freedom) and analysis of variance (table 10) showed that no differences in mortality had resulted from differences in the test variations.

TABLE 12.—*Analysis of variance of the delayed effect (2d to 30th day) of the low (1,000 and 5,000 ohm cm.) and high (10,000 and 15,000 ohm cm.) levels of water resistivity on mortality of fingerling silver salmon*

Source of variation	Sum of squares	Degrees of freedom	Mean square	*F*
Rows [1]	188.5606	3	62.8535	1.377
Low vs. high	153.5121	1	153.5121	3.363
Remainder	35.0485	2	17.5242	0.384
Residual [1]	273.9149	6	45.6525	

[1] See table 10.

CONCLUSIONS

Although analysis of the immediate effect (effect in the first 24 hours) of the conditions tested shows that a significant number of mortalities occurred when the fish were subjected to combinations of two or more of the deleterious variables (low water resistivity, high frequency, and square-wave pulses), it should be remembered, before reading the conclusions of this manuscript, that the fish tested in this experiment were forced to swim completely through the electrical fields created by the array. This situation is not likely to occur in our more successful field experiments, since our method of diverting fish with electricity is based on the principle of an avoidance reaction.

Immediate effect

1. Of the two pulse shapes tested, the square-wave pulses resulted in a higher mortality than the half sine-wave pulses.

2. High frequency (30 p.p.s.) caused a significantly higher mortality than low frequency (15 p.p.s.).

3. Low levels of water resistivity (1,000 and 5,000 ohm cm.) resulted in a higher percentage mortality than the high levels (10,000 and 15,000 ohm cm.).

4. Of the two levels of applied voltage tested, the high voltage (250 v.) resulted in a higher percentage mortality than the low voltage (165 v.). This dif-

ference, however, was not significant at the 5-percent level.

5. The difference between wiring patterns did not cause a significant difference in mortality.

6. A significant difference in mortality between the test fish and the control fish resulted only when two or more of the deleterious variables (square-wave form, low water resistivity, and high frequency) were combined in the tests.

Delayed effect

1. The differences in mortality that could be attributed to the differences between the test variations were not significant after the 30-day holding period.

2. There was no significant difference in mortality between the test fish and the control fish after the 30-day holding period.

In view of these conclusions, it seems logical to infer that, if the electrical shock is going to cause mortalities, most of these mortalities will occur within the first 24 hours after exposure.

SUMMARY

Electricity has been used with some success as a method of diverting fish. However, since its use invariably raises the question of mortality, this experiment was conducted to determine the effect of certain electrical parameters and water resistivities on the mortality of fingerling silver salmon.

A Latin square experimental design was used in the investigation with water resistivity, wiring pattern, pulse shape, voltage, and frequency as variables.

In groups of approximately 100, the fish were subjected to preset electrical and water conditions and then transferred to an outdoor tank where they were held 30 days for observation. Four control groups were also tested for continuous comparison of their mortality with that of the tested fish.

Statistical analysis of the data to determine the immediate (first day) effect of the conditions tested revealed that (1) square-wave pulses resulted in a significantly higher mortality than half sine-wave pulses; (2) high frequency (30 p.p.s.) caused a higher mortality than low frequency (15 p.p.s.); (3) low levels of water resistivity (1,000 and 5,000 ohm cm.) resulted in a higher percentage mortality than high levels (10,000 and 15,000 ohm cm.); (4) although the difference was nonsignificant, high voltage (250 v.) resulted in a higher percentage mortality than low voltage (165 v.); (5) there was no significant difference in mortality that could be attributed to the difference between the two wiring patterns.

A chi-square comparison of the test fish with the control fish revealed that a significant difference in mortality existed only when two or more of the three variables which proved to be deleterious (low water resistivity, square-wave pulses, and high frequency) were combined in the tests.

Effect of the electric shock diminished after the first day; the statistical analysis to determine the delayed effect (second to thirtieth day) revealed that (1) there were no significant differences in mortality that could be attributed to differences between the test variations, and (2) difference in mortality between the test fish and control fish was nonsignificant.

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RELATIONSHIPS AMONG NORTH AMERICAN SALMONIDAE

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This paper is third in a series in which I am attempting to compile and evaluate published information on North American Salmonidae. Definition of the relationship among species is extremely complex and although I would preferably avoid the subject, it must necessarily be considered in order to decide on the grouping of taxa for evaluating the significance of various life-history phases. In such a plastic group as the Salmonidae there are all shades of differentiation from the species down almost to the individual. With our present knowledge, probably the best we can hope to do is to gain some appreciation of the relative closeness of the relationships between taxa.

Basically, we are not so much concerned with whether two populations of any one species of Salmonidae differ phenotypically as we are with their response to similar habitats. Differences in physiological reactions may be just as real as those morphological differences which can be demonstrated statistically.

In our zeal to be objective and quantitative, we must not overlook many of the nonmorphological characteristics that, although perhaps more difficult to assess, nonetheless may show very real differences. I am speaking of such things as color, spawning habits, migratory tendency, growth rate, age at maturity, attainable size, temperature tolerance, and doubtless other yet undefined characteristics inherent in different strains.

The use of such new approaches as serological techniques and paper chromotography may furnish a clue to differences not readily discovered by the classical morphological approach. Counts of the chromosomes, while rendered difficult by the large numbers involved, may be of great taxonomic value, at least at the species levels.

In discussing classification of the Salmonidae it is instructive to commence by observing the relationships among the North American genera. Following the basic work done by Vladykov (1954) we chose tentatively to consider *Cristivomer* as a separate genus, resulting in four North American genera, *Cristivomer*, *Salvelinus*, *Salmo*, and *Oncorhynchus*.

Since all salmonids spawn in fresh water (presumably their ancestral home), the anadromous habit may have evolved gradually from population pressure and a higher survival of fish feeding in the sea.

In the genus *Cristivomer* this seagoing habit (if ever present) is almost if not entirely lost. The genus extends in lakes with sufficient cool oxygenated water in summer (only deep, stratified eutrophic lakes toward the southern part of its range) across North America from arctic Alaska to eastern Quebec. Since it is lacustrine and seldom enters streams, the fact that only one species, *C. namaycush*, covers this entire area might seem a little surprising; usually long-isolated populations tend to develop distinguishable morphologic differences. This lack of differences over such an extended range might be cited to postulate a theory of fairly recent origin for the genus, which however is geologically untenable; but there may be other reasons why differences failed to develop. Differences between isolated populations usually develop through environmental selection. In stream-dwelling fish where environmental differences between localities are often large the selection may be rather severe, but *Cristivomer* inhabits a relatively stable lacustrine habitat that differs little from lake to lake. Furthermore, most geneticists support the postulate (National Research Council, 1956, p. 16) that mutations are induced by naturally occurring radiation: "To the best of our present knowledge, if we increase the radiation by X%, the gene mutations caused by radiation will also be increased by X%."

Folsom and Harley (1957), from data of Libby (1955) and George (1952), have estimated that radiation from cosmic rays at latitudes midway between the geomagnetic equator and 55° N. (geomagnetic) decreases, because of the shielding effect of the water, from 35 millirads per year at the water surface to 10.1 millirads at 10 meters, 4.86 at 20 meters, 1.40 at 50 meters, and only 0.47 millirads per year at 100 meters. Folsom and Harley

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also estimate the internal radiation for a large fish at 28 mrad./year. Thus, whereas a fish living near the surface (in fresh water the radiation activity from the water itself is estimated at less than 0.5 mrad./year) would receive a total of 63 mrad./year, the total dose received would fall rapidly with increasing water depth to 38 mrad. at 10 meters and from 33 to 28.5 mrad./year from 20 to 100 meters. A surface-living lake fish would therefore receive about twice the radiation dose of a fish living below 20 meters.

Most of the salmonids would receive an even heavier radiation dosage than the 63 mrad./year for lake fish at the surface since most of them spend some time in streams, often streams too shallow to afford any shielding effect, in which they would receive additional radiation from the naturally occurring radioactive emitters in the rocks, which varies from about 23 mrad./year for sedimentary rock to about 90 for granite, according to Folsom and Harley.

It has been suggested that in part of their range (i.e., in the deep lakes of the Precambrian shield) lake trout might be subjected to considerable radiation, particularly in the egg stage or during extended periods spent on the bottom. In the absence of data to refute this suggestion it must be considered as a valid criticism of the above hypothesis.

To what extent a lowered mutation rate in *Cristivomer* (which we may perhaps assume from the foregoing discussion of radiation received) could have slowed down the evolutionary processes would be difficult to appraise. An alternate possibility is that *Cristivomer*, during its adaptation to severe conditions in the periods of glaciation that preceded its separation into many isolated colonies, may have lost many of the alleles needed for readaptation to less severe climatic conditions. That this could perhaps be the case is indicated by the ultimate upper lethal temperatures tolerated by various salmonids (Rounsefell, 1958). The young of the other genera all tolerate higher temperatures than the young of *Cristivomer*.

Whether *Cristivomer* or *Salvelinus* is more ancient in origin is a moot question that can be argued from different angles. It could be argued that *Cristivomer* developed from *Cristivomer-Salvelinus* ancestry in North America while *Salvelinus* was simultaneously developing in Asia. Later, perhaps, as conditions ameliorated, *Salvelinus* invaded North America, either over an Asian-North American land bridge, or from the sea. *Cristivomer*, now isolated in deep lakes, unable without the nest building habit to spawn effectively in streams and unable to tolerate the higher temperatures found in most streams, would be unable to make a reciprocal invasion of Asia.

The theory that *Cristivomer* became recognizable in its present form at least as early as the last glacial period is supported by Henshall (1907) writing about the Montana grayling—

> It is very probable that the Arctic grayling was the parent stock from which the Michigan and Montana graylings descended; and from the fact that the habitats of the three species are so widely separated, it is not unreasonable to suppose that the Michigan and Montana forms were conveyed thence from the Arctic regions during the Glacial period. This theory is strengthened by the fact that Elk Lake, a half mile from the Montana grayling station, is abundantly inhabited by both grayling and the lake trout (*Cristivomer namaycush*), which latter fish is found nowhere else west of Lake Michigan.

Salmo might seem to be more ancient in origin than *Oncorhynchus*, which is confined to the North Pacific and Arctic Oceans and is much further adapted toward an anadromous existence. *Salmo* ranges in the western Atlantic from New England to Ungava Bay, thence to southern Greenland and Iceland; in the eastern Atlantic from Portugal to the White Sea. Since *Salmo* (Dymond and Vladykov, 1934) is limited on the western side of the Pacific to the Kamchatka Peninsula, it would not seem likely that it had a Pacific origin. Mottley (1934b) suggests that during the next to the last glacial period the joint ancestors of *Salmo* and *Oncorhynchus* were separated into a Pacific and an Atlantic group, the former evolving into *Oncorhynchus* and the latter into *Salmo*. During the interglacial period, *Salmo* was able to migrate from stream to stream across the continent to the Pacific coast—an impossibility for the strongly anadromous *Oncorhynchus*.

Neave (1958) suggests that *Oncorhynchus* evolved from *Salmo* in the western Pacific, citing in support of his theory the fact that *O. masou* is more primitive than other species of *Oncorhynchus* and is more closely related to *Salmo*. He states—

> In due course the newly evolved offshoot spread back through territories occupied by more conservative lines of the ancestral stock. This process of reinvasion was facilitated by increased adaptation to ocean life and was accompanied or followed by a further splitting up into several species.

None of these explanations suffices to explain fully all of the interrelationships.

There are very few morphological characters by which the various species can be unmistakably identified because—

1. The latitudinal range of many of the species is so wide that the meristic characters, which usually show a latitudinal cline, are quite variable for the same species in different localities (see Mottley, 1934a).

2. For those species with fresh-water forms there is a tendency for the geographically isolated populations to develop slight differences.

3. Anadromous and fresh-water dwelling fish of the same population may show environmental differences in form or coloration. Some of these differences, especially color, have been shown by Wilder (1952) to be reversible in *Salvelinus fontinalis*.

4. In fresh-water forms there may also be altitudinal clines. In some instances, these seem to involve retention of juvenile characteristics. For example, the parr marks in the golden trout, *Salmo gairdneri agua-bonita*, and the piute trout, *Salmo clarki seleniris* (see Snyder, 1940).

The foregoing does not mean that there are not valid species. Any experienced fisherman has no difficulty in separating the five species of Pacific salmon at a glance, even though most individual characters overlap in their range. Species are recognized by a combination of characters and most taxonomic descriptions encompass only a few of those most readily taken and easiest to reduce to numbers.

ATTRIBUTES ANALYZED TO INDICATE RELATIONSHIPS

HYBRIDIZATION

One line of inquiry that yields a clue to interrelationships comes from hybridization experiments. Within recent years several investigators have obtained chromosome counts of salmonids (table 1). In the few species studied, the diploid number ranges from 60 to 84. Of course number alone is not always the controlling factor. Thus, in describing experiments with the crossing of *Salmo salar*, *S. trutta*, *Salvelinus alpinus*, and *S. fontinalis*, Alm (1955) writes—

> The chromosomes of the Brown trout and the Char are, in spite of being the same number, greatly differentiated from one another and the former are more homologous with those of the Salmon. The Brook trout and the Char chromosomes are more in agreement with each other than with the other species.

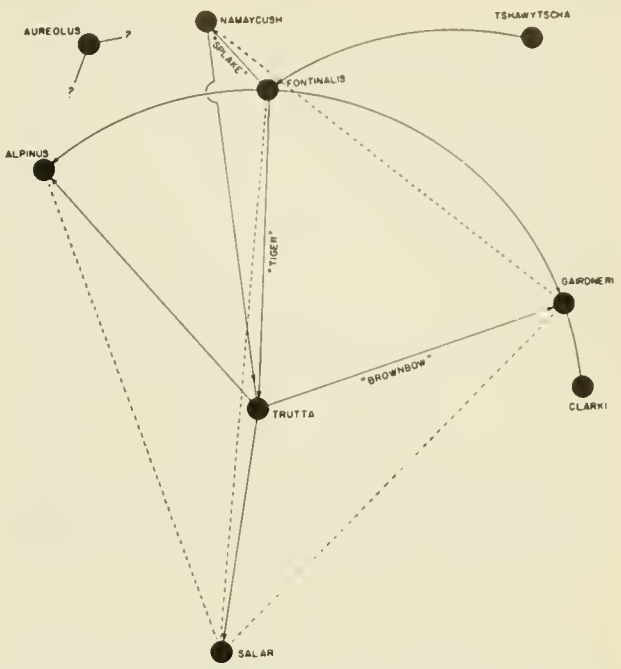

FIGURE 1.—Relative success of crossbreeding of Salmonidae (except *Oncorhynchus*). (Length of solid lines shows relative success; see table 2; dotted lines indicate failure; arrows, direction of male-female cross.)

In comparing *Salmo gairdneri* and *S. salar sebago*, Buss and Wright (1956) noted that "Bungenberg deJong has indicated (1955) a marked difference in the chromosome structure of these species. . . ."

TABLE 1.—*Diploid chromosome number in certain Salmonidae*

Species	Chromosomes	Authority
Salmo salar	60	Svärdson (1945).
Salmo salar sebago	60	Buss and Wright (1956).
Salmo gairdneri	60	Svärdson (1945); Wright (1955).
Salmo trutta	80	Svärdson (1945); Wright (1955).
Salvelinus alpinus	80	Svärdson (1945); Alm (1955).
Salvelinus fontinalis	84	Svärdson (1945); Wright (1955).
Cristivamer namaycush	84	Buss and Wright (1956).
Salmo salar × *Salmo trutta*	70	Svärdson (1945); Alm (1955).
C. namaycush × *S. fontinalis* (= "Splake").	84	Buss and Wright (1956).

From several sources we have compiled table 2 showing the results of certain crosses between species of Salmonidae (*Oncorhynchus* is shown in a separate table). To obtain a clearer view of the results we have rated the success of each cross from 1 to 6 (excellent to failure, see table 2). Although this is subjective, it aids in studying the results which are portrayed in figure 1.

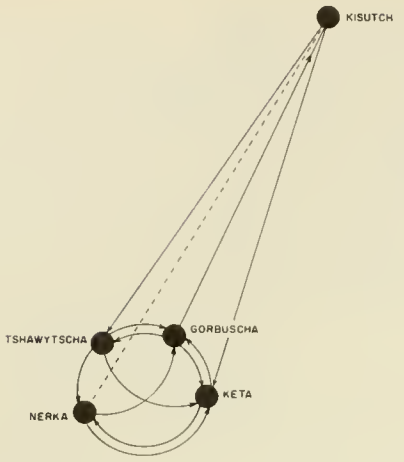

FIGURE 2.—Relative success of crossbreeding of the five eastern Pacific species of *Onchorhynchus*. (Lines indicate relative sucess; see table 3. Arrows indicate direction of male-female cross.)

This figure shows *S. trutta* occupying a position between the Salvelinae and the other species of *Salmo*, approaching closest to *S. salar*. The Salvelinæ appear to be a closely knit group, but not *Salmo*. It is surprising that *trutta* will hybridize, despite the difference in chromosome number with both *salar* and *gairdneri*, yet the latter two so far appear incompatible. No one has been successful in crossing a male *S. gairdneri* with the female of another species, which suggests incompatibility of the male sex chromosome.

The only experiments in crossing *Oncorhynchus* with other Salmonidæ were those of Roosevelt (1880) and Green (1881). In both cases male *O. tshawytscha* from eggs taken in the Sacramento River system were crossed with female *S. fontinalis*, and in both cases hybrids were raised to maturity, but the hybrids were all females, and the eggs would not hatch when fertilized with milt from male *S. fontinalis*.

Within the genus *Oncorhynchus* all five species were crossed in both directions by Foerster (1935); his results are summarized in table 3 and figure 2.

From figure 2, in which the length of each line coincides with the subjective rating of table 3, it is clear that *kisutch* is rather apart from the remainder of the species. This seems to coincide with the conclusions of Milne (1948) from a study of certain morphological characters which will be discussed later. Natural hybrids of *keta* and *gorbuscha* are not uncommon, and Hunter (1949) describes the examination of about 50 such hybrids at Port John, British Columbia; other natural crosses are more rare. The contribution of hybridization toward understanding relationships will have to be evaluated together with other characteristics.

TABLE 2.—*Some interspecific crosses in Salmonidae*

[Excepting *Oncorhynchus*]

Female	Male	Fry survival	Hybrid maturity	Hybrid breeding	Authority	Subjective rating[1]
Salmo salar	*Salmo trutta trutta*	Oood	Low	0	Alm (1955)	3
Do	*S. t. fario*	Low	Low	0	do	5
Do	*Salvelinus alpinus*	0			do	6
Do	*S. fontinalis*	0			do	6
Salmo salar sebago	*Salmo gairdneri*	0			Buss and Wright (1956)	6
Salmo trutta trutta	*Salmo salar*	Fair	Low	0	Alm (1955)	4
S. t. fario	do	Very low	Low	0	do	5
Salmo trutta	*S. salar sebago*	0.3%			Buss and Wright (1956)	5
Do	*C. namaycush*	0.08%			do	5
Do	*Salmo gairdneri*	0			do	6
Do	*Salvelinus fontinalis*	4–5%			do	4
Salmo fario	*S. alpinus*	Very low			Alm (1955)	5
Do	*S. fontinalis*	Low			do	4
Salmo gairdneri	do	0–0.6%			Buss and Wright (1956)	5
Do	*Salmo trutta*	0–1.2%			do	5
Do	do	Very low	Yes	Yes	Stokell (1949)	4
Do	*C. namaycush*	0			Buss and Wright (1956)	6
Do	*Salmo salar sebago*	0			do	6
Do	*S. clarki lewisi*	3%			Simon (1946)	4
Salmo clarki	*Salmo gairdneri*			Naturol	Miller (1950)	1
Salmo gairdneri	*S. clarki*			Hybrids	do	1
Salvelinus fontinalis	*Salmo trutta*	0.5%			Buss and Wright (1956)	5
Do	*Salmo fario*	0			Alm (1955)	6
Do	*S. gairdneri*	0			Buss and Wright (1956)	6
Do	*Salvelinus alpinus*	Low			Alm (1955)	4
Do	*Cristivomer namaycush*	0.7%			Buss and Wright (1956)	5
Do	do	0			Stenton (1950, 1952)	6
Do	*Oncorhynchus tshawytscha*	Fair	Yes	0	Roosevelt (1880); Green (1881)	4
Salvelinus alpinus	*Salmo fario*	Low			Alm (1955)	4
Do	*Salvelinus fontinalis*	Fair		Fair	do	2
Salvelinus aureolus	"Several other chars"			Yes	Vladykov (1954)	
Cristivomer namaycush	*S. fontinalis*	75%	Yes	Good	Stenton (1952)	1
Do	do	28%		10%	Buss and Wright (1956)	1

[1] Subjective ratings of relative success: 1, excellent; 2, good; 3, moderate; 4, poor; 5, very poor; 6, failure.

TABLE 3.—*Results of crossbreeding species of* Oncorhynchus

[First three columns from Foerster, 1935]

Female	Male	Remarks	Subjective rating [1]
tshawytscha	*nerka*	Very poor. 1 fry from 762 eggs	5
Do	*kisutch*	Very poor. Only 15 abnormal fry from 673 eggs.	5**
Do	*keta*	No hatch. Eggs died in early development.	6
Do	*gorbuscha*	Excellent hatch of healthy fry	1*
kisutch	*tshawytscha*	No hatch. Eggs died at the "eyed" stage.	6
Do	*nerka*	Very poor. Only 3 fry from 1,183 eggs	6
Do	*keta*	No fertile eggs recovered	6
Do	*gorbuscha*	Moderate hatch. Fry abnormal	4**
nerka	*tshawytscha*	Excellent hatch of healthy fry	1*
Do	*kisutch*	Only 50 weak alevins from 900 eggs (all died).	6
Do	*keta*	Good hatch of healthy fry	2*
Do	*gorbuscha*	Only 10 fry from 810 eggs (lived only one month).	5
keta	*tshawytscha*	Moderate hatch of healthy fry ("completely successful").	2***
Do	*nerka*	Good hatch of healthy fry	2*
Do	*kisutch*	Very poor. Only 5 fry from 965 eggs	5
Do	*gorbuscha*	166 healthy fry from 1,196 eggs	3*
gorbuscha	*tshawytscha*	Moderate hatch of healthy fry	3*
Do	*nerka*	Moderate hatch (excellent growth of normal individuals).	2*
Do	*kisutch*	No hatch. Eggs died during development.	6
Do	*keta*	Excellent hatch of healthy fry	1*

*Male hybrids matured and bred successfully with *nerka* females.
**Hybrids held to maturity.
***Hybrids presumably held to maturity.
[1] Subjective ratings of relative success: 1 excellent, 2 good, 3 moderate, 4 poor, 5 very poor, 6 failure.

COLORATION

The fact that a great many taxonomic studies have necessarily been made on faded museum specimens has tended to deemphasize the importance of color in classification. Furthermore, the heightening and changing of color in the breeding season contrasted with the hiding of color by the silvery guanin in marine species and even during the lacustrine existence of adfluvial species, has made color a sometimes unreliable tool for field identification in the salmonids. However, there are several color patterns in Salmonidae that may be diagnostic; the genetic inheritance of color in some taxa has been so well documented (for instance in *Lebistes*) that color should be treated with equal or perhaps greater respect than many anatomical characters. In this discussion we are not looking upon color merely as a handy character for identification; therefore, we are comparing coloration under normal conditions. Some of the more evident color characters of adults, not in breeding color, are given in table 4.

The presence on the body of black spots and black speckling characterizes *Oncorhynchus* and *Salmo* with the exception of *S. trutta*, which has both the black spotting and the bright spots otherwise reserved for the charrs. Since none of the charrs (including *Cristivomer*) shows black spotting, *trutta* is intermediate in this character.

Rainbows and cutthroats agree in both the black spotted tail and the bright lateral band. Both characters are absent in *S. salar* and *trutta*.

The dorsal vermiculations are conspicuous in *fontinalis* and faint in *aureolus* and *namaycush*. This close association is corroborated by the hybridization experiments (fig. 1), which showed *fontinalis* closest to *namaycush*.

The parr markings of young Salmonidae are often useful in field identification, despite the considerable variation both in number and shape of the marks (table 5).

Parr marks are absent in *gorbuscha*. This would seem to be associated with the life history since the young pink salmon normally proceed immediately to the sea so that they are in effect not parr, but very small smolts, when they emerge from the gravel. This theory is somewhat strengthened by the fact that *keta*, which is only slightly less anadromous than *gorbuscha* (Rounsefell, 1958), has parr marks which are not as dark as those of *tshawytscha*, *kisutch*, or *nerka*, and which commence fading at an early age.

TABLE 4.—*Normal coloration in adult North American Salmonidae*

Body spots			Caudal fin spots			Bright lateral band	Red streak under maxillary	Vermiculations on back	Black stripe after white edge on lower fins
Black spots	Black and light spots	Light spots	Large black spots	Black speckling	Without black spots				
gorbuscha			*gorbuscha*						
kisutch				*kisutch*					
tshawytscha				*tshawytscha*					
nerka					*nerka*				
keta					*keta*				
gairdneri			*gairdneri*			*gairdneri*			
clarki			*clarki*			*clarki*	*clarki*		
salar					*salar*				
trutta	*trutta*	*trutta*			*trutta*				
		fontinalis			*fontinalis*			*fontinalis*	*fontinalis*
		namaycush			*namaycush*			*namaycush*	
		aureolus			*aureolus*			*aureolus*	
		alpinus			*alpinus*				
		oquassa			*oquassa*				
		malma			*malma*				

TABLE 5.—*Parr marks in young North American Salmonidae*

Species	Number of marks		Shade	Shape	Relation to lateral line	Remarks
	Range	Average				
gorbuscha	0	0				
keta	[1] 6–12 [2] 6–10		Dusky	Elliptical to oval; slender	Chiefly above line	Marks fade at an early age.
tshawytscha	[1] 6–12		Dark	Long vertical bars equal to or wider than interspaces.	Bisected by line.	
kisutch	[1] 8–9		Dark	Narrow vertical bars, about one-half width of interspaces usually narrower than in *tshawytscha*.	Bisected by line	Marks about one-half deptb of body, rounder toward caudal.
nerka	[1] 8–12		Dark	Elliptical to oval	Immediately above line	Row of smaller blotches between parr marks and median dorsal line.
gairdneri [3]	[1] 9–12		Dark	Deep bars, narrower than interspaces.[4]		
trutta				Elliptical, of medium width.[4]	Low on body	Small red blotches between marks.
salar	10–11		Dark	Vertical bars wider than interspaces.		Do.
malma [1]	7–10			Roundish blotches.	On line.	
fontinalis	[5] 7–11	9.0		Large and pear-shaped.[4]		
namaycush [5]	9–11	9.9				
aureolus [5]	11–12	11.7				
marstoni [5]	10–15	12.3				
alpinus [5]	11–15	12.2				

[1] Chamberlain, (1907).
[2] Foerster and Pritchard, (1935b).
[3] Chamberlain (1907) says fry indistinguishable from *S. clarki*.
[4] Bacon (1954, text and plate).
[5] Counts include tbe incomplete bars; Vladykov (1954).

The young of *S. salar* and *trutta* are difficult to distinguish, as are those of *S. gairdneri* and *clarki*. The former agree in the small red blotches between the parr marks, while the latter two have no colored spots but agree in the light lateral band, which is less conspicuous in *clarki*. The hybridization experiments also show *trutta* closer to *salar* than to *gairdneri*.

The aforementioned relation of parr marks to anadromy is indicated by the retention of parr marks throughout life in some landlocked strains of anadromous species. Thus *Salmo gairdneri agua-bonita*, the golden trout, and *Salmo clarki seleniris*, the piute trout, retain their parr marks.

There are a few other color patterns which have from time to time been used to distinguish between certain species or groups. Because information on these color characteristics is lacking for all of the Salmonidae we shall merely mention the characteristic for the groups with such information.

Color of the mouth is used to distinguish *Oncorhynchus* (mouth black) from *Salmo gairdneri* and *clarki*, whose mouths are white (Snyder, 1940; Shapovalov, 1947).

Color of the roof of the mouth is given by Vladykov (1954) as black for *Salvelinus fontinalis*, blackish for *S. aureolus*, and white for *S. oquassa*, *S. marstoni*, *S. alpinus*, and *Cristivomer namaycush*.

ANADROMY

The degree of anadromy exhibited by various taxonomic groups (see Rounsefell, 1958) may well be of phylogenetic significance. Thus, when the degree of anadromy was scored for each species of Salmonidae according to a subjective rating of several criteria it was found that the most anadromous species belonged to *Oncorhynchus*. The next highest rating for anadromy belonged to *Salmo*. Only slight anadromy characterized *Salvelinus*, while *Cristivomer* was lacustrine. The ratings for anadromy are listed in the following table:

Taxon	Rating [1]	Lacustrine	Adfluvial	Fluvial	Anadromous		
					Optionally	Adaptively	Obligatory
Cristivomer	0	*namaycush*					
Salvelinus	7		*oquassa* *o. marstoni*				
	14		*alpinus* *a. aureolus*		*alpinus*		
	12–16		*fontinalis*	*fontinalis*	*fontinalis*		
	18			*malma*	*malma*		
Salmo	21		*trutta*	*trutta*	*trutta*		
	19–20		*clarki* *c. henshawi*	*clarki* *c. seleniris*	*clarki*		
	29		*gairdneri* *g. kamloops*	*gairdneri* *g. agua-bonita*	*gairdneri*		
	34		*salar* *s. sebago*		*salar*		
Oncorhynchus	40–44		*n. kennerlyi*			*nerka*	
	46					*kisutch*	
	47–50						*tshawytscha.*
	54–60						*keta.*
	56–60						*gorbuscha.*

[1] Degree of anadromy (Rounsefell, 1958: p. 180); the rating of a species is partly dependent on the existence of subspecies, which in some cases occupy a different habitat.

MERISTIC CHARACTERS

In using meristic characters to distinguish between any two populations there are certain things to bear in mind. Several investigators have established that in some species some of the meristic characters exhibit phenotypic variation induced by variations in environmental factors during early developmental stages. For a review of these studies see Tåning (1952) and Seymour (1959).

By incubating and rearing chinook salmon, *O. tshawytscha*, at constant temperatures, Seymour (1959) showed that the fish formed the lowest number of vertebrae at intermediate temperatures (45°–55° F.), and higher vertebral numbers at 40° and at 60°. He found, however, that this phenotypic variation was much less than the genotypic variation when lots of eggs from four rivers, the Sacramento, Green, Skagit, and Entiat, were incubated and the fish reared at several constant temperatures. The mean number of vertebrae for all temperatures was about 66 for the Sacramento, 68 for the Skagit, 69 for the Green, and 72 for the Entiat River. As the spawning season in different localities tends to conform to the optimum local conditions, the temperature-induced variation is probably of even less importance than these controlled experiments might suggest. The number of individuals with abnormal vertebrae increased in temperatures above 60° and below 40° F. Seymour also found that low oxygen content of the water during incubation increased the number of vertebrae.

Branchiostegal Rays

Most meristic data on Salmonidae have not been collected in such a manner, or are not sufficiently extensive, as to yield a reliable measure of the range of variation to be expected between samples taken in different years or in different localities. One of the best series of data is from Chamberlain (1907) for sockeye salmon from six streams in the southern portion of southeastern Alaska for the years 1903 and 1904. Since none of his samples had less than 100 individuals we have made an analysis of his data, shown in table 6, for the mean branchiostegal ray counts on 4,686 specimens.

The number of rays is usually higher on the left side as the left membrane normally overlaps the right. Chamberlain states that "In no instance was a clearly defined case of right overlapping seen, though occasionally the right membrane carries the higher number of rays." Similarly, Vladykov (1954, p. 909) found the number of branchiostegals on the right side in all charrs somewhat smaller than on the left.

The analysis of table 6 follows.

TABLE 6.—*Mean count of branchiostegal rays in sockeye salmon, southeastern Alaska, 1903 and 1904*

Locality	Left side		Right side		Total		
	1904	1903	1904	1903	Left side	Right side	Both sides
Quadra	13.579	13.624	13.049	13.092	27.203	26.141	53.344
Yes Bay	13.986	13.930	13.329	13.343	27.916	26.672	54.588
Karla Bay	13.855	13.721	13.339	13.143	27.576	26.482	54.058
Dolomi	13.816	13.800	13.292	13.390	27.616	26.682	54.298
Nowiskay	13.963	13.840	13.384	13.280	27.803	26.664	54.467
Kegan	13.536	13.480	12.931	12.980	27.016	25.911	52.927
Total	82.735	82.395	79.324	79.228	165.130	158.552	323.682
Average: 1904	162.059 $\bar{y}$=13.505				13.761	13.213	13.487
1903	161.623 $\bar{y}$=13.469						

NOTE.—Data from Chamberlain (1907); total of 4,686 specimens, samples of 100 to 513 individuals each.

Source of variation	D.F.	Sum of squares	Mean square	*F*
Total	23	2.423393	0.105365	
Between sides	1	1.802920	1.802920	503.047**
Between years	1	0.007921	0.007921	2.210 N.S.
Between localities	5	0.555203	0.111041	30.982**
Interaction (error)	16	0.057349	0.003584	

The significant difference in the mean number of rays between the left and right sides was confirmed, as well as a significant difference between localities, but the difference between years was very small.

Repeating this analysis, but employing only the number of rays on the left side, a significant difference is again shown between localities, but not between years. If we ignore the possibility of greater differences occurring between years, we still find a maximum mean difference for the left side of 0.506 rays between samples (13.986–13.480). This suggests use of great caution in forming conclusions about interspecific differences in a meristic character on the basis of small samples, especially if the samples are not geographically representative.

If one compares this mean branchiostegal count for *O. nerka* from southeastern Alaska with the average given by Foerster and Pritchard (1935a)

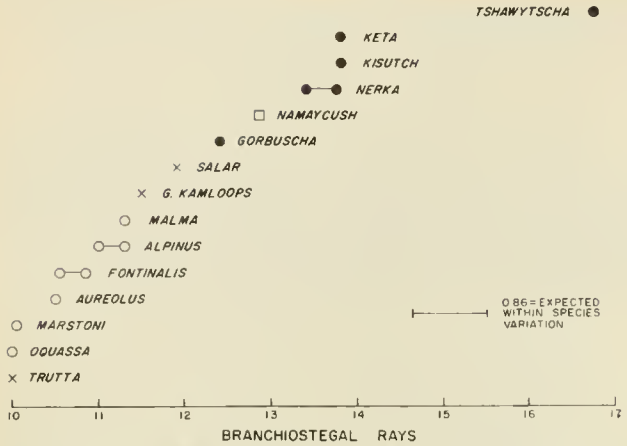

FIGURE 3.—Mean numbers of branchiostegal rays.

for British Columbia and Puget Sound the difference is 0.354. Considering that a difference of 0.506 was noted between adjacent localities in southeastern Alaska, it would seem logical to add this geographical difference of 0.354 to the previous difference of 0.506, which gives a difference of 0.860 rays that can be expected between means of samples of the same species.

The branchiostegal ray counts for various Salmonidae are summarized in table 7 and figure 3. If we apply to the other species the criterion found above for *nerka* of an expected "within species" difference of 0.86 rays between samples we find that the table clearly sets apart *O. tshawytscha*. The next three species of *Oncorhynchus*, *keta*, *kisutch*, and *nerka* are close together but separated from *gorbuscha*.

C. namaycush is clearly distinct from the remaining charrs.

Another interesting point is that *S. trutta* is quite separate from *salar* or *g. kamloops*. This is reminiscent of the position of *S. trutta* (in fig. 1) between the charrs and the other *Salmo*.

TABLE 7.—*Count of branchiostegal rays on left side in North American Salmonidae*

[x in frequency column indicates rays present, but no numbers given]

Species	Number of rays												Number of specimens	Mean number of rays	Standard error
	8	9	10	11	12	13	14	15	16	17	18	19			
Oncorhynchus:															
gorbuscha [1]			8	30	136	121	22	2					319	12.392	0.053
nerka [1]				2	22	128	106	17					275	13.415	.052
Do [2]				2	131	1,420	2,545	569	19				4,686	13.769	.010
kisutch [1]					1	51	50	25					127	13.780	.071
keta [1]					4	52	49	27	3				135	13.800	.077
tshawytscha						1	0	13	43	69	18	9	153	16.758	.083
Salmo salar [3]			x	x	x								65		
salar [4]													41	11.9	
gairdneri [5]			x	x	x										
g. kamlocps [6]													213	11.51	.040
clarki [5]			x	x	x										
trutta [4]													41	10.0	
Salvelinus:															
fontinalis [7]		1	19	27	12								59	10.847	.098
Do [8]	1	21	190	193	45								450	10.578	.035
alpinus [7]			3	6	3								12	11.0	
Do [9]													37	11.3	.380
oquassa [7]			4										4	10.0	
aureolus [7]		2	13	17	2								34	10.559	.080
marstani [7]		4	34	5									43	10.023	.103
malma [9]													57	11.3	.30
Cristivomer:															
namaycush [7]					6	28	2						36	12.889	.244

[1] Foerster and Pritchard (1935a); Puget Sound and British Columbia.
[2] Chamberlain (1907); southeastern Alaska.
[3] Kendall (1935, p. 137).
[4] McCrimmon (1949); eastern Canada.
[5] Shapovalov (1947).
[6] Mottley (1936); Kootenay Lake.
[7] Vladykov (1954).
[8] Wilder (1952); Nova Scotia and New Brunswick.
[9] DeLacy and Morton (1943); Kariuk, Alaska.

Pyloric Caeca

Since more material is available for *Oncorhynchus* it has been considered first (table 8). The published material on caeca is usually listed by categories and since different authors have used different breaking points for their categories, some of their material may be listed slightly in error; thus, the number of caeca if listed from 96–105 would be given in table 8 under the category 95–104.

The material for *tshawytscha* is extremely variable but this is caused chiefly by the great difference between the counts for the Sacramento River

(Suisun Bay) and those for the Klamath River. These two samples by McGregor (1923) are the highest and lowest in caecal count. I suspect that this variability is caused by some extraneous factor. When the Klamath River counts are separated into those caught at Requa at the mouth of the river and those taken at the salmon counting weir, 170 miles upstream at Klamathon, the weir-caught salmon show a much lower count. Possibly, the upstream count was lowered on account of the atrophy of the digestive tract prior to spawning.

TABLE 8.—*Number of pyloric caeca in species of* Oncorhynchus

Number of caeca	Number of specimens of—											
	kisutch	*nerka*	*gorbuscha*					*tshawytscha*				
	Milne (1948) [1]	Milne (1948) [1]	Milne (1948) [1]	Pritchard (1945) [2]	Pritchard (1945) [3]	Pritchard (1945) [4]	Sum	Milne (1948) [1]	Townsend (1944) [5]	Townsend (1944) [6]	Townsend (1944) [7]	Townsend (1944) [8]
45–54		1										
55–64	1	6										
65–74	8	15										
75–84	3	30										
85–94	3	40						1				
95–104	1	27	1			5	6					
105–114	1	3	4	49	3	16	72			1		
115–124			7	116	23	65	211				1	4
125–134			8	148	22	95	273		5	7	5	17
135–144			12	119	21	76	228	1	8	14	4	26
145–154			4	77	16	54	151		12	12	21	32
155–164			4	21	8	26	59	1	10	26	9	17
165–174			1	7	2	6	16	2	7	26	11	14
175–184						3	3	1	6	22	11	4
185–194				2		1	3	1	2	6	4	3
195–204								1		4	3	1
205–214										2		
215–224			1				1			1	1	
225–234										1		
235–244									1	1		
245–254												
Number of specimens	17	122	42	539	95	347	1,023	8	51	123	70	118
Mean number of caeca	75.5	85.5	136.3	133.5	137	135.9	134.75	155.0	157.5	165.8	162.5	150.5

Number of caeca	Number of specimens of—							Percentage distribution				
	tshawytscha (con.)						*keta*					
	McOregor (1923) [9]		McGregor (1923) [10]	Parker (1943) [11]	Parker (1943) [12]	Sum	Milne (1948) [1]	*kisutch*	*nerka*	*gorbuscha*	*tshawytscha*	*keta*
	a	b										
45–54									0.8			
55–64								5.9	4.9			
65–74								47.1	12.3			
75–84								17.6	24.6			
85–94		1				2		17.6	32.8		0.2	
95–104		1				1		5.9	22.1	0.6	0.1	
105–114	2	3				6		5.9	2.5	7.0	0.7	
115–124	7	6			3	23				20.6	2.8	
125–134	12	6	2	7	7	69				26.7	8.3	
135–144	9	4	3	22	12	101				22.3	12.1	
145–154	9	3	8	40	14	150				14.8	18.0	
155–164	1		13	43	13	133				5.8	15.9	
165–174			10	48	25	143				1.6	17.1	
175–184			14	31	11	100	4			0.3	12.0	20
185–194	2		18	20	7	63	2			0.3	7.5	10
195–204			10	8	2	29	3				3.5	15
205–214			3	2	3	10	4				1.2	20
215–224						2	5			0.1	0.2	25
225–234						1	1				0.1	5
235–244						2					0.2	
245–254							1					5
Number of specimens	42	24	81	221	97	835	20					
Mean number of caeca	137.5	126.2	176	165.7	162.7	160.68	205.0					

[1] Skeena River, British Columbia.
[2] Queen Charlotte Islands (7 streams).
[3] Vancouver Island, Morrison Creek.
[4] Lower Fraser River (5 streams).
[5] Cowlitz River, Wash.
[6] Middle Fork, Willamette River, Oreg.
[7] McKenzie River, Oreg.
[8] South Santiam River, Oreg.
[9] Klamath River (a, at Requa, mouth of river; b, at Klamathon racks, 170 miles upstream).
[10] Sacramento River.
[11] Sacramento River.
[12] Sacramento and San Joaquin Rivers.

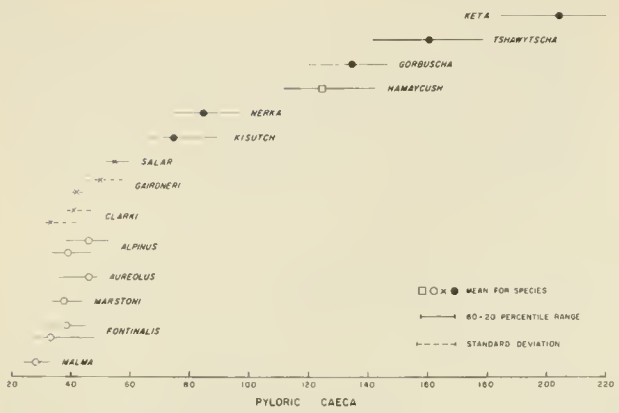

FIGURE 4.—Mean numbers of pyloric caeca. (Lines indicate the 20th and 80th interpercentile range.)

If we disregard McGregor's samples the intraspecific variation in the mean caecal count is small, ranging from 150.5 to 165.8 for *tshawytscha* and from 133.5 to 137 for *gorbuscha*. This is a small range in relation to that for the five species—from 75.5 for *kisutch* up to 205.0 for *keta*.

The data for the remaining genera are far less extensive so they are combined with the summary for *Oncorhynchus* in table 9. In figure 4 the means are given as well as the approximate 20th and 80th percentiles. Obviously, *Oncorhynchus* and *Cristivomer* differ markedly from *Salmo* and *Salvelinus* in number of caeca.

In number of pyloric caeca, as in number of branchiostegal rays, *C. namaycush* differs markedly from *Salvelinus* and is close to *Oncorhynchus*.

TABLE 9.—*Count of pyloric caeca in North American Salmonidae*

Species	Range in number [1]		Approximate percentiles		Mean number of caeca	Number of specimens
	Minimum	Maximum	Q20	Q80		
Oncorhynchus: [2]						
kisutch	55	114	67	90	75.5	17
nerka	45	114	75	97	85.5	122
gorbuscha	95	224	120	147	134.8	1,023
tshawytscha	85	244	142	179	160.7	835
keta	175	249	185	221	205.0	20
Salmo:						
salar [3]	40	74	(4)	(4)	55.4	561
gairdneri [5]	25	54	35	50	42	11
Do.[6]	39	61			50	16
clarki [6]	27	40			33	11
Do.[7]	23	60			40.3	71
Salvelinus:						
fontinalis [8]	20	49	33	45	38.4	30
Do.[9]	23	46	27	38	32.5	47
malma [9]	20	39	24	32	27.9	114
alpinus [9]	30	64	38	53	46.0	62
Do.[8]	20	59	33	47	39.1	16
aureolus [8]	30	[10] 99	34	49	45.9	35
oquassa [8]					39	1
marstoni [8]	20	49	33	44	37.7	34
Cristivomer:						
namaycush [9]	95	170	112	143	126.7	55

[1] Upper and lower limits of groups unless given by authors.
[2] References for *Oncorhynchus* in table 8.
[3] Belding (1940); eastern Canada.
[4] Standard deviation, 4.03.
[5] Milne (1948); Skeena River.
[6] Townsend (1944); Oregon.
[7] DeWitt (1954); northern California.
[8] Vladykov (1954).
[9] Morton and Miller (1954); presumably these data include counts for *malma* and *alpinus* by DeLacy and Morton (1943), Karluk, Alaska.
[10] Only 1 specimen beyond category of 70–79; distribution extremely skewed.

Fin Rays

The comparison of fin-ray counts is rendered difficult by differences in counting methods used by different investigators. For instance, for the anal fin counts of *O. nerka* in table 10, Foerster and Pritchard (1935a, p. 91) write—

> In counting fin rays only developed rays, those which had attained a length of one-half the length of the longest ray, were included. The remainder were considered as undeveloped. Care was taken to ensure that branched rays did not lead to error in the count.

Milne (1948) apparently used the same method since he comments (p. 73) concerning his difference in average count between 1946 and 1947—

> . . . it is possible although not probable, that during the first year (1946) less attention was focussed on omitting rays less than one-half the length of the fin or in counting branched rays as two with the result that a higher count might have been recorded in error for 1946.

Chamberlain (1907, p. 89) writes—

> In the fin-ray counts the totals of rudimentary and branched rays are used, but the terminal half ray, which varies greatly in development, is in all cases omitted.

It will be noted that the counts for *O. nerka* given by Chamberlain are about 3 rays higher than the others, owing doubtless to his inclusion of the rudimentary rays. A good summary of this difficulty is given by Vladykov (1954, p. 911), who writes—

> . . . there are technical difficulties in counting small simple rays in front of the dorsal and anal fins. The best way is to remove the skin and stain the rays with alizarin. In larger specimens the stained fins should be dissected and made transparent by placing in glycerine. To avoid error in counting these small rays in unstained specimens, some authors, as Kendall (1914, p. 24), counted only "fully-developed" rays in the dorsal and anal fins. Unfortunately there is no definition of the term "fully-developed." Some other authors count only branched rays, which are plainly seen even without staining with alizarin. Unfortunately the number of branched rays in younger fish (parr) is smaller than in older individuals of the same species . . . .

TABLE 10.—*Count of anal fin rays in* O. nerka

Locality	Number of specimens with fin ray count of—									Number of specimens	Mean number of rays	Year
	12	13	14	15	16	17	18	19	20			
Southeastern Alaska: [1]												
Quadra					2	56	277	167	8	[2] 510	18.24	1904
Do						65	276	146	10	497	18.20	1903
Yes Bay					3	82	322	97	5	509	18.04	1904
Do					1	42	207	49	1	300	18.02	1903
Karta Bay					1	133	307	71		512	17.88	1904
Do					1	114	268	37		420	17.81	1903
Kegan				1	6	150	315	38		510	17.75	1904
Do					2	32	56	8	2	100	17.76	1903
Dolomi					10	248	238	15		511	17.51	1904
Do					13	85	96	6		200	17.48	1903
Nowiskay				1	33	257	212	9	1	513	17.39	1904
Do					7	44	46	3		100	17.45	1903
Sum:												
1904				2	55	926	1,617	397	14	3,065	17.80	
1903					24	382	949	249	13	1,617	17.90	
Both years				2	79	1,308	2,620	646	27	4,682	17.84	
Unweighted average:												
1904											17.80	
1903											17.79	
Both years											17.80	
Skeena River, British Columbia: [3]												
Prince Rupert		1	4	36	60	1	1			103	15.57	1946
Do		3	27	39	17					86	14.81	1947
Moricetown		5	42	18	2					67	14.25	1946
Do		2	11	17	11		1			42	14.98	1947
Babine		5	14	8	3					30	14.30	1946
Do		1	9	4						14	14.21	1947
Lakelse		1	8	3						12	14.71	1946
Do	2	4	5	4						15	13.73	1947
Sum:												
1946		12	68	65	65	1	1			212	14.90	
1947	2	10	52	64	28		1			157	14.70	
Both years	2	22	120	129	93	1	2			369	14.81	
Unweighted average:												
1946											14.57	
1947											14.43	
Both years											14.50	
Southern British Columbia, and Puget Sound [4]		4	53	38	8					103	14.49	Mixed

[1] From Chamberlain (1907).
[2] Because published data by Chamberlain is in percentages a few of the samples reconverted to actual numbers differ slightly from original sample size, undoubtedly owing to rounding off of percentages.
[3] From Milne (1948).
[4] From Foerster and Pritchard (1935a).

In determining how much variation to expect between anal-ray counts within a species (table 10) we can only compare counts made by the same investigator. In Chamberlain's data, the maximum difference between sample means is 0.85 (18.24−17.39). In Milne's (1948) data we can compare only the 1947 data (see quotation above) which leaves a difference of 1.25 (14.98−13.73). Because of the small size of the Lakelse sample this difference may be too large.

A comparison of the means and ranges of the anal-ray count in table 11 shows that counts in all *Oncorhynchus* are definitely higher than in the other genera. *Salmo gairdneri* occupies an intermediate position between *Oncorhynchus* and the charrs.

For dorsal rays, as for the anal, counting methods differed between investigators. Table 10 indicates that Foerster and Pritchard (1935a) were counting about 3 less anal rays than Chamberlain was. The dorsal-ray count appears to vary somewhat less than the anal-ray count; thus, for Chamberlain's data on southeastern Alaska sockeye the maximum difference between sample means is 0.85 rays for the anal-fin count but only 0.51 for the dorsal count (table 12).

TABLE 11.—*Count of anal fin rays in North American Salmonidae*

[Counts adjusted to a complete count (see text); x indicates rays present in frequency column but no number given]

Species	Number of specimens with anal-ray count of—															Number of specimens	Mean number of rays
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22		
Oncorhynchus:																	
nerka [1]								2	79	1,308	2,620	646	27			4,682	17.84
Do.[2]								2	22	120	129	93	1	2		369	17.81
Do.[3]									4	53	38	8				103	17.49
gorbuscha [2]										8	49	54	20			131	18.66
Do.[3]									4	34	190	76	3			307	18.13
kisutch [2]								5	8	24	21	2				60	17.12
Do.[3]								4	37	55	10	3				109	16.73
keta [2]									1	5	18	12	2			38	18.24
Do.[3]									24	64	36	11	2			137	17.29
tshawytscha [2]									1	9	26	26	13	1		76	18.58
Do.[3]											18	60	20		1	99	19.05
Salmo:																	
gairdneri [4]					12	15	3	1								31	13.77
Do.[5]				x	x	x	x										
g. kamloops [6]																215	12.90
clarki [5]				x	x	x											
salar [7]		x	x	x												65	
trutta [8]		x	x	x													
Cristivomer:																	
namaycush [9]			2	12												14	10.86
Salvelinus:																	
fontinalis [10]		4	111	274	66											455	10.88
Do.[9]	3	8	9	2												22	9.46
oquassa [9]				1												1	11.00
marstoni [9]		5	15	16	2											38	10.39
aureolus [9]		8	13	3												24	9.79
alpinus [9]		8	7	3												18	9.72
Do.[11]																57	9.0(?)
malma [11]																63	9.0(?)

[1] Chamberlain (1907); southeastern Alaska; complete count made.
[2] Milne (1948); Skeena River; data adjusted by adding 3 rays (see table 10).
[3] Foerster and Pritchard (1935a); southern Britisb Columbia and Puget Sound; data adjusted by adding 3 rays (see table 10).
[4] Milne (1948); Skeena River; data adjusted by adding 2 rays (McCrimmon (1949) says 1 rudimentary and 1 unbranched in *S. salar* and *S. trutta*).
[5] Shapovalov (1947); California; 2 rays added.
[6] Mottley (1936); Kootenay Lake, British Columbia; 2 rays added; standard deviation 0.5.
[7] Kendall (1935, p. 137); Penobscot River; 2 rays added; McCrimmon (1949).
[8] McCrimmon (1949); count includes rudimentary rays.
[9] Vladykov (1954); complete count.
[10] Wilder (1952); Nova Scotia; complete count.
[11] DeLacy and Morton (1943); Karluk, Alaska; count may be incomplete.

TABLE 12.—*Count of dorsal fin rays in* O. nerka

Locality	Number of specimens with fin ray count of—										Number of specimens	Mean number of rays	Year
	9	10	11	12	13	14	15	16	17	18			
Southeastern Alaska:[1]													
Quadra					12	225	265	11	1	1	515	14.55	1904
Do					13	212	256	19			500	14.56	1903
Yes Bay					9	211	274	13	2		509	14.58	1904
Do					5	109	183	2	1		300	14.62	1903
Karta Bay					3	162	312	35			512	14.74	1904
Do					2	122	265	30	1		420	14.78	1903
Kegan					13	277	211	10			511	14.43	1904
Do					2	57	40	1			100	14.40	1903
Dolomi				1	13	274	211	10			509	14.42	1904
Do					6	107	82	5			200	14.43	1903
Nowiskay					28	299	175	10			512	14.33	1904
Do					7	61	30	2			100	14.27	1903
Sum:													
1904				1	78	1,448	1,448	89	3	1	3,068	14.51	
1903					35	668.	856	59	2		1,620	14.58	
Both years				1	113	2,116	2,304	148	5	1	4,688	14.53	
Unweighted average:													
1904												14.51	
1903												14.51	
Southern British Columbia and Puget Sound [2]	1	12	66	23	2						104	11.13	

[1] Chamberlain, 1907. Because his published data are in percentages, a few of the reconstructed samples differ slightly in sample number.
[2] Foerster and Pritchard, (1935a); counts do not include all rays.

The meager data on dorsal-ray counts for all species are summarized in table 13, in which I have attempted to adjust all data to a complete count. This shows that the overlap in the frequency distributions of the dorsal-ray count is sufficiently large that many individuals of *Oncorhynchus* can not be distinguished from the charrs on the basis of dorsal-ray count.

It is worthy of note that *O. kisutch* is lower than the remaining *Oncorhynchus* in both anal- and

dorsal-ray counts, suggesting a closer approach to the other genera. This coincides with the distant relation of *kisutch* to the other *Oncorhynchus* species as shown in figure 2.

TABLE 13.—*Count of dorsal fin rays in North American Salmonidae*

[Count adjusted to complete count (see text); x indicates rays present in frequency column, but numbers not given]

Species	Number of specimens with dorsal ray count of—										Number of specimen	Mean number of rays
	9	10	11	12	13	14	15	16	17	18		
Oncorhynchus:												
nerka [1]				1	113	2,116	2,304	148	5	1	4,688	14.53
Do.[2]				1	12	66	23	2			104	14.13
gorbuscha [2]					3	69	210	24			306	14.83
kisutch [2]				3	26	61	19				109	13.88
keta [2]					5	47	82	3			137	14.61
tshawytscha [2]					1	32	54	11	1		99	14.79
Salmo:												
salar [3]				x	x	x						
trutta [3]				x	x	x						
gairdneri [4]				x	x	x	x					
g. kamloops [5]											216	13.08
clarki [4]		x	x	x	x							
Cristivomer:												
namaycush [6]		2	8	4							14	11.14
Salvelinus:												
fontinalis [7]		2	90	268	93	2					455	12.01
Do.[6]	3	11	6	2							22	10.32
oquassa [6]				1							1	12.00
marstoni [6]		2	16	20	1						39	11.51
aureolus [6]	1	8	12	3							24	10.71
alpinus [6]	1	4	6	6							17	11.00
Do.[8]											57	10.00
malma [8]											64	10.50

[1] Chamberlain (1907), southeastern Alaska, complete count.
[2] Foerster and Pritchard (1935a), southern British Columbia and Puget sound, data adjusted by adding 3 rays.
[3] McCrimmon (1949).
[4] Shapovalov (1947), 2 rays added.
[5] Mottley (1936), Kootenay Lake, British Columbia (2 rays added, standard deviation, 0.5.
[6] Vladykov (1954), complete count.
[7] Wilder (1952), Nova Scotia, complete count.
[8] DeLacy and Morton (1943), Karluk, Alaska, count may be incomplete

Vertebrae

Because the methods used in counting vertebrae vary, it is difficult to place all counts on a common basis. Vladykov (1954) says that "all vertebrae were counted, including three of the hypural." DeLacy and Morton (1943) state "In the up-turned posterior end of the vertebral column the fused vertebrae were counted as one." Wilder (1952) says "In counting the vertebrae the urostyle was excluded."

Obviously, vertebral counts of different investigators may differ by as much as three vertebrae, according to their method of recording. To place all counts on a comparable basis (using the total count) some of the published counts must be increased by either two or three vertebrae. Data on vertebral counts are meager. Mottley (1937) gives data, shown in table 14, which include counts for all of the North American *Salmo*.

TABLE 14.—*Count of vertebrae in genus* Salmo

[Counts from Mottley, 1937]

Species	Number of specimens with vertebral count of—											Number of Specimens	Mean Number of vertebrae	Variance	Standard deviation	Standard error
	57	58	59	60	61	62	63	64	65	66	67					
gairdneri [1]							14	10	1			25	63.48	0.35	0.59	0.117
g. kamloops [2]						4	22	21	3			50	63.46	.53	.73	.104
Do.[3]								12				12	64.00	.0	.0	
Do.[4]						4	10	8	3			25	63.40	.83	.91	.183
Do.[5]						1	7	11	5	1		25	63.92	.83	.91	.182
Do.[6]						1	5	6	5			17	63.88	.86	.93	.225
Do.[7]							13	12				25	63.48	.26	.51	.102
Do.[8]							2	11	9	2	1	25	64.56	.85	.92	.184
g. whitehousei [9]						7	17	17	6	2		49	63.57	1.04	1.02	.146
Do.[10]						6	25	15	4			50	63.34	.44	.66	.093
Do.[11]							4	11	6	4		25	64.40	.92	.96	.191
clarki [11]					1	12	10	2				25	62.52	.50	.71	.143
trutta [12]	3	12	9	1								25	58.32	.56	.75	.150
salar [13]		5	15	4	1							25	59.04	.53	.73	.147

[1] Cowichan River, Vancouver Island, 1931; reared at Cowichan hatchery.
[2] Redfish Creek, 1930.
[3] Lardeau River, 1930.
[4] Penask Lake, 1930; reared at Nelson hatchery.
[5] Paul Creek, 1931.
[6] Paul Lake, 1931; reared at Lloyd's Creek hatchery.
[7] Paul Lake, 1932.
[8] Paul Lake, 1932; reared at Lloyd's Creek hatchery.
[9] 6-mile Lake, 1930.
[10] 6-mile Lake, 1930; reared at Nelson hatchery.
[11] Cottonwood Lake, 1930; reared at Nelson hatchery.
[12] Wisconsin stock, 1931; reared at Cowichan hatchery.
[13] From Thurso River, Scotland, 1933; reared at Cowichan hatchery.

Mottley's counts are chiefly on fry or fingerlings 20 to 75 mm. in length. He stained the tissues with alizarin and counted the last stained centrum; since the urostyle did not stain it was not counted. He writes—

> In making a comparison with the data of other investigators, however, it should be noted that in the caudal region, if the centra were stained as discrete blocks they were counted separately, if the separation was not complete they were counted as one.

Because the last two or three vertebrae were not always separated in the very small fish, he found a slight tendency toward a lower vertebral count in the smaller fry. Therefore, although his data can be used for interspecific comparisons in *Salmo*, they must be used cautiously in making comparisons with species of other genera.

The maximum mean difference between any 2 of the 11 samples of *Salmo gairdneri* is 1.22 vertebrae (64.56 minus 63.34). Obviously *S. gairdneri* and *clarki* differ significantly from either *salar* or *trutta*. Whether *clarki* and *gairdneri* or *salar* and *trutta* can be distinguished by vertebral count cannot be answered without additional data.

For the genus *Oncorhynchus*, all available counts except those for two small samples of adult *tshawytscha* were made by Foerster and Pritchard (1935b) on unstained young ranging from 7/8 inch to 3 inches in length. According to their statement it would appear that their counts do not include the three upturned vertebrae in the tail. Furthermore, there is some reason to suspect that the number counted is related to size. Table 15 gives the estimate of the statistical parameters for the five species and it may be noted that the variance was highest (7.84) for *nerka*, which has the smallest fry, and smallest (2.20 and 1.44, respectively) for *gorbuscha* and *tshawytscha*, which have the largest fry.

For *nerka*, the distribution of vertebral counts is negatively skewed so that the mean, 63.73, is about 2 counts below the mode (about 65.5). In the bottom part of table 15 are shown the resulting estimates of the parameters for four species of *Oncorhynchus*, when the counts causing this extreme negative skew are disregarded. Although *tshawytscha* shows the highest average count it would seem unwise to use vertebrae as a distinguishing character between species of *Oncorhynchus* until further data are available.

TABLE 15.—*Count of vertebrae in genus Oncorhynchus*

Number of vertebrae	Number of young (7/8 to 3 in.)[1]					Number of adult[2] *tshawytscha*		Sum of *tshawytscha*
	nerka	*kisutch*	*keta*	*gorbuscha*	*tshawytscha*	McKenzie River	Willamette River	
56	2							
57								
58	2	1						
59	3	1	1					
60	3	5		1				
61		5	3					
62	6	2	2					
63	9	18	2	1				
64	5	*21*	7	2				
65	12	10	8	14	1	1		2
66	*13*	5	*21*	11	1	6		7
67	7		17	*16*	2	2	7	11
68			6	4	15		9	24
69				1	*25*		6	31
70					18			18
71					6			6
72					1			1
Number of specimens	62	68	67	50	69	9	22	100
Mean number of vertebrae	63.73	63.29	65.57	66.00	69.10	66.11	67.95	68.58
Variance	7.84	3.11	3.61	2.20	1.44	.37	.62	1.98
Standard deviation	2.80	1.76	1.90	1.48	1.20	.61	.79	1.41
Standard error	.359	.214	.232	.210	.145	.204	.130	.141
Range[3]	62–67	62–66	62–68	63–69				
Number	52	56	63	49				
Mean	64.73	63.96	65.89	66.12				
Variance	2.54	1.02	2.04	1.48				
Standard deviation	1.59	1.01	1.43	1.22				
Standard error	.220	.142	.180	.174				

NOTE. Believe these are 3 vertebrae short of total number, as Foerster and Pritchard say, ". . . the segments beginning with the one immediately behind the skull and ending with the one immediately in front of the long vertebrae projecting up into the tail can be counted".

[1] Foerster and Pritchard (1935b); Cultus Lake, British Columbia, except *gorbuscha* which were from Masset Inlet, British Columbia.

[2] Townsend (1944); Oregon.

[3] Recapitulation of estimated sample parameters rejecting counts below 62 vertebrae (see text).

Vladykov (1954) does not give the source of his samples of *Salvelinus* (table 16) but comparison of the variances and ranges of his sample counts with those of Mottley suggests (table 17) that each of his individual samples may not be from one locality. The great variation in both ranges and variances casts doubt on the utility of making any but very broad generalizations from these available data, and also casts serious doubt on the utility of using normal probability estimates for describing distributions of discrete variables that have such a small range.

Salvelinus fontinalis, apparently, is significantly lower in vertebral count than either *C. namaycush* or other species of *Salvelinus*.

The extremely large variances (table 17) in some of the samples of *Oncorhynchus* are apparently caused by undercounting in the smaller fry. Therefore, in table 18 the adjusted values are used for four of the species of *Oncorhynchus*.

The values for the vertebral counts are summarized in figure 5, which shows that the count is highest in *Oncorhynchus* and lowest in *Salmo salar*, *S. trutta*, and *Salvelinus fontinalis*. All of the other species occupy an intermediate position with respect to this character.

TABLE 16.—*Count of vertebrae in* Salvelinus *and* Cristivomer

[x indicates vertebrae present in frequency column, but no numbers given]

Species	Number of specimens with vertebral count of —												Number of specimens	Mean number of vertebrae	Variance	Standard deviation	Standard error
	58	59	60	61	62	63	64	65	66	67	68	69					
S. alpinus [1]				1	1	4	0	3	2	5			16	64.81	4.16	2.04	0.510
Do.[2]								x	x	x	x	x	53	66.7	1.54	1.24	.17
S. marstani [1]			1	1	1	5	13	7	2				30	63.90	1.69	1.30	.237
S. aureolus [1]				1	3	2	5	7					18	63.78	1.72	1.31	.308
S. oquassa [1]									1				1	66			
S. malma [2]					x	x	x	x	x				37	64.3	1.06	1.03	.17
S. fontinalis [1]	2	5	4	1	1								13	59.54	1.28	1.13	.312
Do.[3]													25	59.68			
Do.[4]													24	60.04			
C. namaycush [1]				1	8	7	4	2	1				23	63.04	1.49	1.22	.255

[1] Vladykov (1954).
[2] DeLacy and Morton (1943); Karluk River, Alaska; count increased by 2 to include all vertegrae.
[3] Wilder (1952); anadromous stock, Moser River, Nova Scotia; count increased by 3 to include all vertegrae.
[4] Wilder (1952); resident stock, Moser River, Nova Scotia; count increased by 3 to include all vertegrae.

TABLE 17.—*Ranges and variances of vertebral-count distributions*

[Presumably individual samples]

Count	Mottley (1937)	Townsend (1944)	DeLacy and Morton (1943)	Vladykov (1954)	Foerster and Pritchard (1935b)	All authors	Foerster and Pritchard adjusted[1]	Total using adjusted values
Range:								
0	1					1		1
1	1					1		1
2	1	2				3		3
3	8					8		8
4	3		2	2		7		8
5				1		1	1	2
6				2		2	2	4
7					1	1	1	1
8					1	1		
9					2	2		
10						0		
11					1	1		
Average range	2.8	2.0	4.0	5.0	8.0	4.3	5.6	3.7
Variance:								
0–0.40	3	1				4		4
0.41–0.80	5	1				6		6
0.81–1.20	6		1			7	2	9
1.21–1.60			1	2	1	4	1	4
1.61–2.00				2		2		2
2.01–2.40					1	1	1	1
2.41–2.80						0	1	1
2.81–3.20					1	1		
3.21–3.60						0		
3.61–4.00					1	1		
7.81–8.00					1	1		

[1] See bottom of table 15.

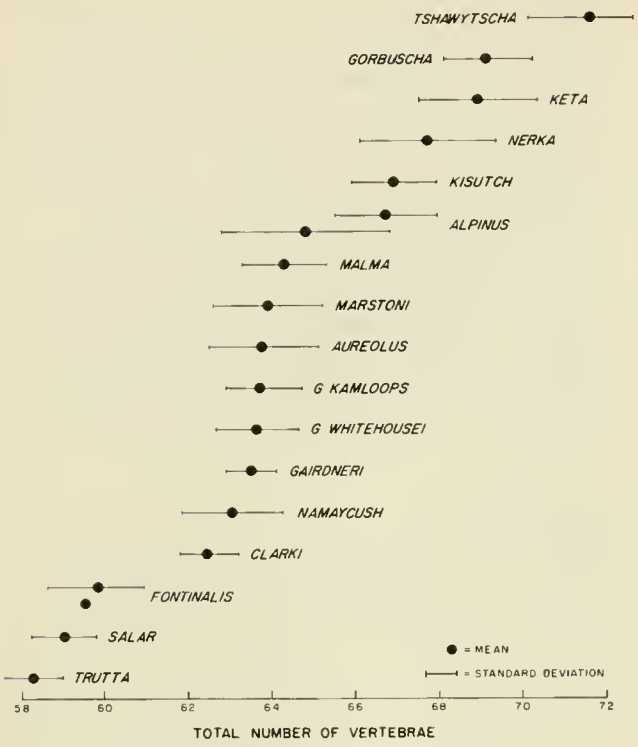

FIGURE 5.—Mean number of vertebrae.

Gill rakers

Counts of gill rakers made by different investigators are somewhat more comparable than are those of the vertebral counts. Even here, however, there seems to be some question concerning the comparability of counts between fish of different sizes. Thus Wilder (1952, p. 187) says that all the gill rakers on both limbs of the first gill arch were counted including rudimentary rakers sometimes present on large trout. He also writes that—

> The exceptionally low raker count for Bocabec trout is possibly a result of the low average size (115 mm. SL) of the fish in this sample as there is some evidence to indicate that raker count increases with size in salmonoids. . . .

Foerster and Pritchard (1935b) write concerning young *Oncorhynchus*—

> From Table 1, in which is presented a summary of the average numbers of gill-rakers for each ⅛-inch length group for all species, it appears that in the very early stages up to a length of 1¾ inches, there is an increase in the number of gill-rakers with increase in size. Such a change might be attributed to the overlooking of some of the rudimentary rakers on the very small arches, but in view of the fact that all counts were carefully made under comparatively high magnification, it is unlikely that such an error would have occurred.

The available gill-raker counts for *Oncorhynchus* are given in table 19. Obviously, the count of *O. nerka* is significantly higher than that of *gorbuscha*, which in turn is significantly higher than the counts of the remaining three species. Because the counts for *Oncorhynchus* are all for mature adults returning from the sea on a spawning migration, the factor of size of fish on gill-raker count may be entirely disregarded.

If we disregard the two smaller samples of *tshawytscha* (14 and 17 specimens), the largest differences between means of samples of the same

TABLE 18.—*Number of vertebrae in North American Salmonidae*

Species	Number of specimens	Mean number of vertebrae	Adjusted values [1]		Unadjusted range			Standard deviation [2]	Standard error [2]
			Number	Mean	Minimum	Maximum	Total		
Oncorhynchus:									
tshawytscha	100	71.58			68	75	7	1.41	0.141
gorbuscha	50	69.00	49	69.12	63	72	9	1.22	.174
keta	57	68.57	63	68.89	62	71	9	1.43	.180
nerka	62	66.73	52	67.73	59	70	11	1.59	.220
kisutch	68	66.29	56	66.96	61	69	8	1.01	.142
Salmo:									
gairdneri kamloops	179	63.75			62	67	5	.87	.065
g. whitehousei	124	63.65			62	66	4	.99	.090
gairdneri	25	63.48			63	65	2	.59	.117
clarki	25	62.52			61	64	3	.71	.143
salar	25	59.04			58	61	3	.73	.147
trutta	25	58.32			57	60	3	.75	.150
Salvelinus:									
alpinus	53	66.7			65	69	4	1.24	.17
Do	16	64.81			61	67	6	2.04	.510
malma	37	64.3			62	66	4	1.03	.17
marstoni	30	63.90			60	66	6	1.30	.237
aureolus	18	63.78			61	65	4	1.31	.308
fontinalis	13	59.54			58	62	4	1.13	.312
Do	49	59.86							
Cristivomer:									
namaycush	23	63.04			61	66	5	1.22	.255

[1] See bottom part of table 15 for treatment of these data.
[2] Based on adjusted values for *Oncorhynchus*.

NOTE.—Insofar as possible was put on basis of total number of vertebrae; for details see tables 15–17.

species are 1.78 for *gorbuscha* and 1.19 for *nerka*, which gives us some basis for judging the differences between the means of the much smaller samples of the other genera. The distributions of gill-raker count are given for *Salmo*, *Salvelinus*, and *Cristivomer* in table 20.

TABLE 19.—*Number of gill rakers on first gill arch (left side) in* Oncorhynchus

Number of gill rakers	Number of specimens of—													
	nerka						*gorbuscha*							
	Foerster and Pritchard (1935a) [1,2]	Milne (1948) [3,4]	Milne (1948) [3,5]	Milne (1948) [4,6]	Milne (1948) [6,8]	Sum	Foerster and Pritchard (1935a) [7,8]	Milne (1948) [4,6]	Milne (1948) [5,6]	Pritchard (1945) [9,10]	Pritchard (1945) [10,11]	Pritchard (1945) [12,13]	Pritchard (1945) [12,14]	Sum
24								2			1			3
25								2						2
26								3			1			4
27							3	8	1		6	2	2	22
28		1				1	20	14	1	1	18	10	18	82
29							70	22	4	13	65	22	91	287
30	1	1		1	1	4	111	24	11	23	118	38	146	471
31	2	3		1		6	79	9	15	37	110	23	125	398
32	6	2	3	2	1	14	30	2	8	21	55	8	62	186
33	18	8	6	5	4	41	5	1	5	3	10		10	34
34	51	19	16	9	6	101		1	1	1	1		3	7
35	74	15	20	23	9	141					1			1
36	72	15	14	24	22	147								
37	48	14	10	20	11	103								
38	32		8	10	10	60								
39	13			3	2	18								
Number of specimens	317	78	77	98	66	636	318	88	46	99	386	103	457	1497
Mean number of rakers	35.62	34.72	35.27	35.73	35.91	35.52	30.11	29.11	30.89	30.78	30.34	29.91	30.35	30.23

Number of gill rakers	Number of specimens of—									Percentage distribution				
	tshawytscha				*keta*			*kisutch*						
	Foerster and Pritchard (1935a) [1,2]	Milne (1948) [6,16]	Townsend (1944) [16]	Sum	Foerster and Pritchard (1935a) [1,2]	Milne (1948) [6,16]	Sum	Foerster and Pritchard (1935a) [1,17]	Milne (1948) [6,15]	Sum	*nerka*	*gorbuscha*	*tshawytscha*	*keta*	*kisutch*
19						1	1	4	1	5				0.5	3.3
20	3	4		7	2	2	4	3	5	8			3.8	2.1	5.3
21	10	1		11	15	5	20	14	8	22			6.0	10.6	14.6
22	32	3		35	36	14	50	37	7	44			19.0	26.6	29.1
23	45	6	2	53	60	13	73	50	5	55			28.8	38.8	36.4
24	43		4	47	34	2	36	13		13		0.2	25.5	19.1	8.6
25	12		6	18	3		3	14		4		0.1	9.8	1.6	2.6
26	6		1	7	1		1					0.3	3.8	0.5	
27	1	2	1	4								1.5	2.2		
28	1	1		2							0.2	5.5	1.1		
29												19.2			
30											0.6	31.5			
31											0.9	26.6			
32											2.2	12.4			
33											6.4	2.3			
34											15.9	0.5			
35											22.2	0.1			
36											23.1				
37											16.2				
38											9.4				
39											2.8				
Number of specimens	153	17	14	184	151	37	188	125	26	151					
Mean number of rakers	23.22	22.76	24.64	23.28	22.81	22.14	22.68	22.45	21.38	22.26					

[1] Puget Sound to Butedale, British Columbia.
[2] 1925, 1926, 1934.
[3] Prince Rupert, British Columbia.
[4] 1946.
[5] 1947.
[6] Skeena River and tributaries, British Columbia.
[7] Fraser River to northern British Columbia.
[8] 1928, 1930, 1932, 1934.
[9] Morrison Creek, Vancouver Island, British Columbia.
[10] 1941.
[11] Four tributaries of lower Fraser River, British Columbia.
[12] 1940.
[13] Two Moresby Island streams, Queen Charlotte Islands, British Columbia.
[14] Five streams in Masset Inlet, Graham Island, Queen Charlotte Islands, British Columbia.
[15] 1946, 1947.
[16] McKenzie River, Oregon.
[17] 1934.

TABLE 20.—*Count of gill rakers on first gill arch, left side, in* Salmo, Salvelinus, *and* Cristivomer

[x indicates gill rakers present in frequency column, but numbers not given]

Species	Number of specimens	Number of specimens with raker count of—														Mean number of rakers
		14	15	16	17	18	19	20	21	22	23	24	25	26	27	
Salmo:																
salar [1]	65				x	x	x	x	x							
Do.[2]	41															19.8
trutta [2]	41															17.0
gairdneri [3]	28			1		1	10	9	5	2						19.75
g. kamloops [4]	214															19.34
clarki [5]		x	x	x	x	x	x	x	x							
Salvelinus:																
alpinus [6]	9				1	1	1	1	2		1			1	1	21.3
Do.[7]	71								x	x	x	x	x	x		23.4
malma [7]	62		x	x	x	x	x	x	x	x						18.1
oquassa [6]	1									1						
marstoni [6]	38					2	5	13	12	5	1					20.4
aureolus [6]	16		1	4	1	2	3	1	2		1	1				18.6
fontinalis [6]	50			15	13	9	5	4	2	2						17.7
Do.[8]	171	1	10	31	53	42	28	6								17.36
Do.[9]	150	2	14	35	35	33	20	10	1							17.25
Do.[10]	29	2	2	10	6	5	3	1								16.79
Total *fontinalis*	400	5	26	91	107	89	56	21	3	2						17.32
Cristivomer namaycush [6]	25						7	10	9		1					20.2

[1] Kendall (1935); Penobscot River.
[2] McCrimmon (1949).
[3] Milne (1948); Skeena River, British Columbia.
[4] Mottley (1936); Kootenay Lake, Britisb Columbia.
[5] Shapovalov (1947).
[6] Vladykov (1954).
[7] DeLacy and Morton (1943); Karluk River, Alaska.
[8] Wilder (1952); anadromous stock, Moser River, Nova Scotia.
[9] Wilder (1952); resident stock, Moser River, Nova Scotia.
[10] Wilder (1952); from 3 brooks in Nova Scotia. Sample from Bocabec Brook in New Brunswick omitted because of small size of the fish.

The gill-raker counts of tables 19 and 20 are summarized in table 21, in which I have endeavored to give some indication of dispersion. Many of the samples were so small, with the distribution either discontinuous or skewed, that the standard deviation was discarded and instead I have shown the range and the interpercentile range from the 80th to the 20th percentile (see fig. 6).

It is interesting to note that *trutta* shows the lowest average for gill rakers (fig. 6), as it also does for branchiostegal rays and vertebrae (fig. 3 and 5). *Fontinalis*, which is next to the bottom in gill-raker count, occupies the same position for number of pyloric caeca and is quite low in number of branchiostegal rays and vertebrae.

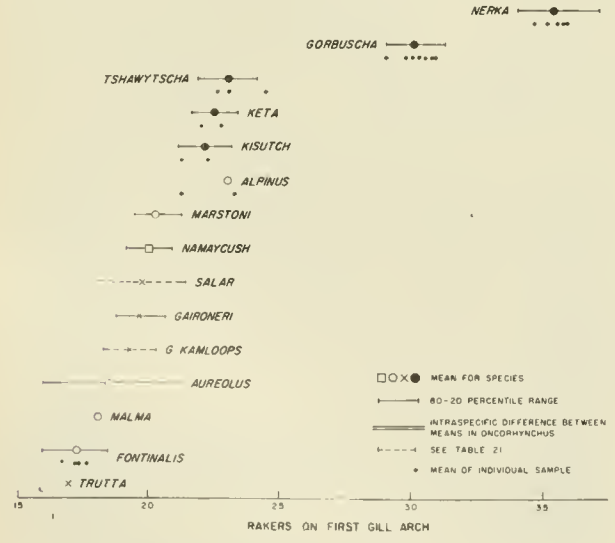

FIGURE 6.—Gill rakers on first gill arch.

The question of gill rakers on other than the first gill arch will be discussed later.

Scales

Although scale counts are widely used in taxonomic work they must be used cautiously because of the variation in counting practice among different investigators. Neave (1943) gives an excellent discussion of the various counting methods in vogue. One difficulty arises from the failure of many authors to recognize that the number of scales in the lateral line does not usually correspond either to the number of diagonal (oblique) rows just above the lateral line or to the number of diagonal rows counted along any horizontal row several rows above the lateral line. As a result many published data on the count of lateral-line scales, or "scales along the lateral line," actually refer to a count of diagonal rows made either just above the lateral line (usually a somewhat higher count) or of diagonal rows counted several longitudinal rows above the lateral line (usually a still higher count).

Some investigators have varied these practices by counting the lateral-line tubes or sensory pores and considering them equal in number to lateral-line scales. A fifth method has been to count the rows of diagonal scales 10 or 15 rows above the

TABLE 21.—*Summary of gill-raker count of North American Salmonidae*

[First gill arch, left side]

Species	Number of specimens	Mean number of gill rakers	Range		Percentile			Total range
			Minimum	Maximum	20	80	80–20	
Oncorhynchus:								
nerka	636	35.52	28	39	34.10	37.32	3.12	11
gorbuscha	1,497	30.23	24	35	29.11	31.35	2.24	11
tshawytscha	184	23.28	20	28	22.04	24.28	2.24	8
keta	188	22.68	19	26	21.75	23.56	1.81	7
kisutch	151	22.26	19	25	21.28	23.26	1.98	6
Salmo:								
salar	41	19.8	17	21	[1] (18.1)	[1] (21.5)	[1] 3.36	4
trutta	41	17.0						
gairdneri	28	19.75	16	22	18.86	20.78	1.92	6
g. kamloops	214	19.34			[2] (18.4)	[2] (20.3)		
clarki			14	21				7
Salvelinus:								
alpinus [3]	9	21.3	17	27	18.5	25.5	7.00	10
Do.[4]	71	23.4	21	26				
malma	62	18.1	15	22				
marstoni	38	20.4	18	23	19.55	21.37	1.82	5
aureolus	16	18.6	15	24	16.05	21.40	5.35	9
ontinalis [5]	50	17.7	16	22	16.17	19.10	2.93	6
Do.[6]	171	17.36	14	20	16.25	18.50	2.25	6
Do.[6]	150	17.25	14	21	15.90	18.55	2.65	7
Do.[7]	29	16.79	14	20	15.68	18.14	2.46	6
Total, *fontinalis*	400	17.32	14	22	16.03	18.54	2.51	8
Cristivomer:								
namaycush	27	20.2	19	23	19.27	20.99	1.72	4

[1] Standard deviation of 1.6 multiplied by 2.1. McCrimmon (1949) gives 1.6 as standard error of mean for *salar* and 0.01 as standard error of mean for *trutta*. The first must be standard deviation, the second is improbably small since standard deviation would be only 0.06.

[2] Assuming same interpercentile range as for *S. gairdneri* above.

[3] Eastern Canada.

[4] Karluk River, Alaska.

[5] Anadromous stock, Moser River, Nova Scotia.

[6] Resident stock, Moser River, Nova Scotia.

[7] Three small brooks in Nova Scotia.

FIGURE 7.—Number of lateral-line scales.

lateral line from the gill aperture to the adipose fin and, then, to continue the count at a lower level from the adipose fin to the caudal. The five methods are briefly summarized as follows, in the order of usually increasing count:

1. Number of sensory pores on lateral line.
2. Number of scales on lateral line.
3. Number of diagonal scale rows in the horizontal row just above the lateral line.
4. Number of diagonal scale rows from top of gill aperture to caudal.
5. Number of diagonal scale rows from top of gill aperture to caudal, counting on a lower horizontal row posterior to adipose fin.

Most investigators terminate the count at the base of the caudal fin (standard length), but some count the scales that extend on to the caudal fin.

Available counts of lateral-line scales (methods 1 and 2) are summarized in table 22 and in figure 7.

It is obvious from figure 7 that the variation between the mean numbers of lateral-line scales from different localities (and perhaps between counts by different investigators) is so great that only a few of the species can be separated by this character. However, there is a general trend with species of *Oncorhynchus* the highest, and *fontinalis*, *salar*, and *trutta* the lowest counts.

TABLE 22.—*Counts of scales in lateral line of North American Salmonidae*

Species	Number of specimens	Mean number of scales	Range			Percentile			Year
			Minimum	Maximum	Total	20	80	80–20	
Oncorhynchus:									
gorbuscha [1]	254	172	148	198	50	163	179	16	
Do [2]	41	184	160	198	38	175	189	14	1946–47
Do [3]	3	166	147	180	33				
tshawytscha [1]	133	140	130	153	23	135	145	10	
Do [2]	41	146	130	165	35	142	150	8	1946–47
Do [3]	9	134	130	138	8				
keta [1]	155	136	124	153	29	131	140	9	
Do [2]	27	139	130	147	17	135	142	7	1946–47
Do [3]	6	133	129	139					
nerka [1]	145	131	124	138	14	128	133	5	
Do [4]	50	135	127	141	14	132	138	6	1946
Do [4]	76	133	130	141	11	132	137	5	1947
Do [5]	46	140	124	150	26	137	143	6	1946
Do [6]	42	135	124	141	17	130	135	5	1947
Do [6]	37	130	124	138	14	127	133	6	1946–47
Do [7]	20	134	127	141	14	131	137	6	1946–47
Do [3]	10	129	122	135					
Do [8]	3,068	133.1	126	143	17	132	135	3	1904
Do [8]	1,612	133.3	127	141	14	132	135	3	1903
kisutch [1]	127	129	121	138	17	127	131	4	
Do [2]	27	136	130	144	14	133	138	5	1946
Do [2]	24	134	130	141	11	131	137	6	1947
Do [3]	10	128	123	132	9				
Salmo;									
salar [9]	11	111	106	113	7				
Do [10]	41	111							
gairdneri [11]	122	124	119	131	12	122	126	4	
Do [12]	61	120	114	124	10	118	121	3	
Do [2]	23	130	124	138	14	127	132	5	1946–47
Do [13]	11	122	119	125	6				
g. kamloops [14]	25	126	121	130	9	124	128	4	
Do [9]	1	128							
clarki [15]	50	123	116	133	17	120	126	6	
Do [16]	30	120	116	126	10	117	122	5	
Do [17]	6	122	120	129	9				
Do [18]	13	119	116	126	10				
trutta [9]	11	112	107	117	10				
Do [12]	25	112	105	116	11	110	114	4	
Do [10]	41	112							
Cristivamer:									
namaycush [3]	19	125	121	130	9				
Salvelinus;									
alpinus [3]	12	122	111	130	19				
fontinalis [3]	28	115	109	127	18				
malma [3]	18	126	120	131	11				

[1] Foerster and Pritchard (1935a); Fraser River to northern British Columbia.
[2] Milne (1948); Skeena River, British Columbia.
[3] Morton and Miller (1954); count is of sensory pores.
[4] Milne (1948); Prince Rupert, British Columbia.
[5] Milne (1948); Moricetown, Skeena River, British Columbia.
[6] Milne (1948); Babine Lake, Skeena River, British Columbia, in 1946 and 1947.
[7] Milne (1948); Lakelse Lake, Skeena River, British Columbia, in 1946 and 1947.
[8] Chamberlain (1907); tubes on lateral line continued onto caudal for 6 localities in southeastern Alaska.
[9] Morton and Miller (1954); count is of lateral line scales.
[10] McCrimmon (1949).
[11] Neave (1943); anadromous stock, Cowichan River, British Columbia.
[12] Neave (1943); resident stock, Cowichan River, British Columbia.
[13] Morton and Miller (1954); resident stock, Rush Creek, Modoc County, Calif.
[14] Neave (1943).
[15] Neave (1943); reared at Cowichan Lake Hatchery, Vancouver Island, British Columbia.
[16] Neave (1943); reared at Veitch Creek Hatchery, Vancouver Island, British Columbia.
[17] Morton and Miller (1954); coastal strains of Oregon and Washington.
[18] Morton and Miller (1954); *S. c. pleuriticus* from Colorado River Basin.

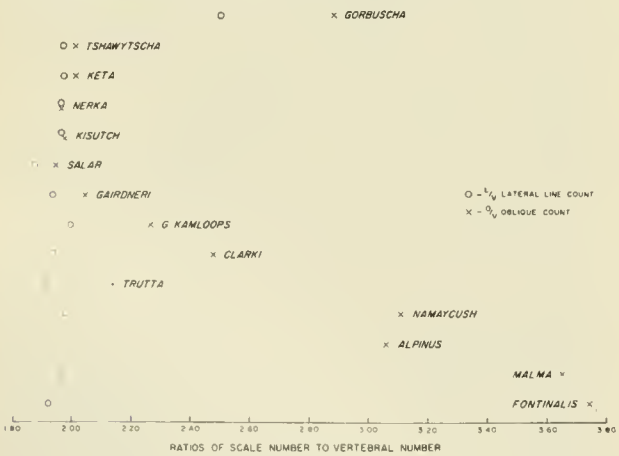

FIGURE 8.—Relation between numbers of vertebrae and scales.

Before commenting further on this character, in table 23 we have compiled the numbers of oblique scale rows counted (with exceptions noted) along the first row of scales above the lateral line. In discussing the lateral scale count, it is instructive to compare the results of counts made on the lateral line and counts made one row (or more) above the lateral line. This comparison is shown in table 24 and figure 8.

It may be noted in comparing the number of vertebrae (fig. 5) with the number of lateral-line scales (fig. 7) that the different species maintain approximately the same ranking in the two characters (see table 24). Even though for several of the species the vertebral counts and scale counts are not all—in some cases none—from the same

TABLE 23.—*Number of diagonal (oblique) scale rows in first row above the lateral line in North American Salmonidae*

Species	Number of specimens	Mean number of rows	Range			Percentile		
			Minimum	Maximum	Total	20	80	80–20
Oncorhynchus:								
gorbuscha [1]	195	199	169	231	62	190	209	19
Do [2]	8	213	194	226				
tshawytscha [1]	110	143	133	153	20	138	148	10
Do [2]	47	149	138	158				
keta [1]	135	139	130	153	23	136	142	6
Do [2]	5	141	137	145	8			
nerka [1]	173	133	124	144	20	129	137	8
Do [2]	16	138	130	146				
kisutch [1]	124	131	118	147	29	127	134	7
Do [2]	9	138	133	145				
Salmo:								
salar [2]	11	115	111	118				
gairdneri [3]	122	132	123	159	36	128	136	8
Do [4]	61	122	115	130	15	119	125	6
Do [5]	8	137	125	149	24			
Do [6]	11	154	146	164	18			
g. kamloops [7]	25	143	130	155	25	134	150	16
Do [2]	1	148						
Do [8]	216	145	130	160	30	140	151	11
clarki [7]	50	160	146	177	31	154	166	12
Do [9]	30	137	122	154	32	128	143	15
Do [10]	6	165	157	170	13			
Do [11]	13	191	180	208	28			
Do [12]	78	152	122	188	66			
trutta [2]	11	125	120	131	11			
Do [4]	25	125	116	136	20	121	131	10
Cristivomer:								
namaycush [2]	30	196	175	228	53			
Salvelinus:								
alpinus [2]	28	195	154	236	82			
Do [13]	15	217	195	236	41			
malma [2]	31	231	186	254	68			
Do [13]	13	243	218	254	36			
fontinalis [2]	25	218	197	236	39			
Do [14]	83	225	200	243	43	217	232	15

[1] Foerster and Pritchard (1935a); Fraser River to northern British Columbia.
[2] Morton and Miller (1954).
[3] Neave (1943); anadromous stock, Cowichan River, British Columbia.
[4] Neave (1943); resident stock, Cowichan River, British Columbia.
[5] Morton and Miller (1954); anadromous stock, Clackamas River, Oreg.
[6] Morton and Miller (1954); resident stock, Rush Creek, Modoc County, Calif.
[7] Neave (1943); reared at Cowichan Hatchery, Vancouver Island, British Columbia.
[8] Mottley (1934a); Kootenay Lake, several rows above lateral line.
[9] Neave (1943); reared at Veitch Creek Hatchery, Vancouver Island, British Columbia.
[10] Morton and Miller (1954); coastal streams of Oregon and Washington.
[11] Morton and Miller (1954); *S. c. pleuriticus*, from Colorado River Basin.
[12] DeWitt (1954); northern California coastal streams, counted along second scale row above lateral line.
[13] DeLacy and Morton (1943); Karluk Lake, Alaska.
[14] Wilder (1952); Moser River, Nova Scotia, count is from posterior margin of head to end of vertebral column (presumably several scale rows above the lateral line).

TABLE 24.—*Comparison of number of vertebrae and number of lateral-line scales, in North American Salmonidae*

Species	Mean number of—			L/V	O/V
	Vertebrae [1] (V)	Lateral-line scales [2] (L)	Scales in first row above lateral line (O)		
Oncorhynchus:					
gorbuscha	69.12	173.7	199.6	2.51	2.89
tshawytscha	71.58	141.4	144.8	1.98	2.02
keta	68.89	136.4	139.1	1.98	2.02
nerka	67.73	133.3	133.4	1.97	1.97
kisutch	66.29	130.7	131.5	1.97	1.98
Salmo:					
salar	59.04	111.0	115.0	1.88	1.95
gairdneri	63.48	123.4	130.4	1.94	2.05
g. kamloops	63.75	126.1	144.8	2.00	2.27
clarki	62.52	121.5	155.0	1.94	2.48
trutta	58.32	112.0	125.0	1.92	2.14
Cristivomer: namaycush	63.04	125.0	196.0	1.98	3.11
Salvelinus:					
alpinus	66.26	122.0	202.7	1.84	3.06
malma	64.3	126.0	234.5	1.96	3.65
fontinalis	69.79	115.0	223.4	1.92	3.74

[1] From table 18, weighted means.
[2] Weighted mean, excluding counts of sensory pores where lateral-line scale count is available.

samples or localities, the scale count (L) closely approaches twice the vertebral count (V) with one notable exception. The lateral-line scale count for *O. gorbuscha* is 2.5 times the vertebral count.

Neave (1943) noted this anomaly in *O. gorbuscha* and wrote—

> After examining a few small pink salmon fingerlings the present writer believes that the first scale papillae show the same distribution as in other species but that subsequently papillae develop between the primary members of the lateral line series, as well as dorsad and ventrad to the latter. This development can perhaps be correlated with the comparatively large size attained by this species before scale formation begins, resulting in a wider spacing between the sense organs and thus leaving room for the establishment of papillae.

This close relation (except in *gorbuscha*) between vertebral count and lateral-line scale count (approximately twice the verterbral count) is

depicted in figure 8. Since these two characters are not independent they should not be used independently in any racial analysis involving a "character" index. The relation between number of vertebrae and number of oblique scale rows (O/V in fig. 8) on the other hand shows that there is a wide variation in the degree of branching of the lateral-line scale papillae: *malma* and *fontinalis* with an O/V ratio of 3.65 and 3.74, respectively, represent the extreme in fine scaling; *alpinus* and *namaycush* with O/V ratios of 3.06 and 3.11 form another distinct group; *gorbuscha*, with an increase in both types of scale counts, occupies a unique position. All of the species of *Salmo* show a slight to moderate increase in the number of oblique scale rows over the number of lateral-line scales.

Surprisingly, in view of the position of *gorbuscha*, the other species of *Oncorhynchus* show no detectable increase in number of oblique scale rows over their lateral-line scale counts.

The number of horizontal scale rows is available for so few species that counts for all genera are combined in table 25. The data for *Salmo salar* and *S. trutta* differ in the method of counting and these species cannot be compared with the others. The published values of 0.82 and 0.16, given presumably as standard errors of the mean for *salar* and *trutta*, differ widely. This suggests strongly that the number of specimens whose scales were counted (at least for *salar*) was much less than the 41 given by McCrimmon (1949). It is therefore doubtful whether the means for the two species should be considered significantly different without additional data.

TABLE 25.—*Number of horizontal scale rows in certain species of Salmonidae*

Species	Number of specimens	Mean number of rows	Range			Percentile			Year
			Minimum	Maximum	Total	20	80	80–20	
FROM ANTERIOR OF DORSAL FIN TO LATERAL LINE									
Oncorhynchus:									
gorbuscha [1]	320	34.3	26	40	14	32	37	5	
Do.[2]	16	33.4	27	37	10	32	35	3	1946
Do.[2]	25	36.7	33	40	7	35	38	3	1947
tshawytscha [1]	135	30.8	27	37	10	29	33	4	
Do.[2]	21	30.9	23	37	14	30	32	2	1946
Do.[2]	16	30.7	26	35	9	30	32	2	1947
kisutch [1]	127	26.5	23	31	8	25	28	3	
Do.[2]	25	27.4	24	31	7	25	29	4	1946
Do.[2]	22	27.5	23	30	7	26	30	4	1947
keta [1]	154	22.9	19	31	12	21	25	4	
Do.[2]	14	25.5	22	32	10	24	27	3	1946
Do.[2]	12	24.1	22	26	4	23	26	3	1947
nerka [1]	183	21.8	18	26	8	21	23	2	
Do.[3]	47	22.5	18	24	6	20	23	3	1946
Do.[3]	76	22.4	19	27	8	21	23	2	1947
Do.[4]	63	22.8	21	26	5	22	24	2	1946
Do.[4]	16	22.2	20	24	4	22	24	2	1947
Do.[5]	22	22.0	19	24	5	21	23	2	1946–47
Do.[6]	16	23.6	22	26	4	23	24	1	1946–47
Salmo:									
gairdneri [2]	23	25.5	22	30	8	23	27	4	1946–47
Salvelinus:									
malma [7]	15	42.0						[8] 2.8	1939–41
alpinus [7]	15	34.0						[8] 3.7	1939–41
FROM ANTERIOR OF VENTRAL (PELVIC) FIN TO LATERAL LINE									
Oncorhynchus:									
gorbuscha [1]	319	32.4	25	40	15	30	35	5	
tshawytscha [1]	109	30.0	23	39	16	27	33	6	
kisutch [1]	127	25.7	19	37	18	24	28	4	
nerka [1]	113	21.5	17	27	10	20	22	2	
keta [1]	155	21.4	17	27	10	19	24	5	
Salvelinus:									
malma [7]	15	42.1						[8] 2.8	1939–41
alpinus [7]	15	35.7						[8] 3.7	1939–41
FROM POSTERIOR BASE OF ADIPOSE FIN TO LATERAL LINE									
Salmo:									
salar [9]	41	10.8						[10] 0.82	
trutta [9]	41	15.2						[10] 0.16	

[1] Foerster and Pritchard (1935a); Fraser River to northern British Columbia.
[2] Milne (1948); Skeena River, British Columbia.
[3] Milne (1948); Prince Rupert, British Columbia.
[4] Milne (1948); Moricetown, Skeena River, British Columbia.
[5] Milne (1948); Babine Lake, Skeena River, British Columbia.
[6] Milne (1948); Lakelse Lake, Skeena River, British Columbia.
[7] DeLacy and Morton (1943); Karluk Lake, Alaska.
[8] Standard deviation.
[9] McCrimmon (1949).
[10] These values are presumably the standard error of the mean, but for *salar* the error is inexplicably large if the number of specimens is 41 as stated by McCrimmon (1949, p. 11).

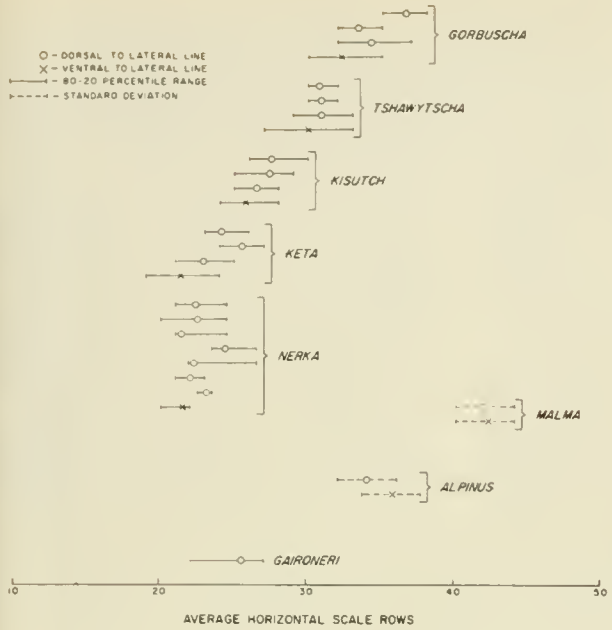

FIGURE 9.—Number of horizontal scale rows.

The average horizontal scale counts for *Oncorhynchus*, two species of *Salvelinus*, and *Salmo gairdneri* are shown in figure 9. *Malma* has the largest number, followed by *alpinus* and *gorbuscha*. The variation in number of scales within species is large, the maximum between means for *gorbuscha* being 3.3 in the number of scale rows above the lateral line.

Despite large differences in the sample means a definite trend exists in *Oncorhynchus* from the fine-scaled *gorbuscha* to the relatively coarse-scaled *keta* and *nerka*.

ANALYSIS OF MERISTIC CHARACTERS

All meristic characters were placed on a common basis to facilitate their comparison. Such a basis was established by determining the lowest and highest species means for any given character and then using the numerical difference between the two means as a yardstick. The lowest mean has been rated as 0, the highest as 10, and the intermediate means have been rated in between according to their position on the scale. The ranking of characters is given by species in table 26.

As explained earlier, not all of these characters are independent variables. Therefore, if we use two closely correlated characters in attempting to weigh differences between species from several characters, we are in effect giving double weight to the same measure. Figures 10 to 12 show the close correlation between three pairs of characters.

To obtain a joint ranking of these pairs of correlated characters, the rankings were adjusted (table 27) according to a correction factor (table 26) to equalize the average ranking for the species with available data. After obtaining the joint rankings for three pairs of correlated meristic characters, we are left with six presumably independent meristic rankings, which are listed by species in table 28.

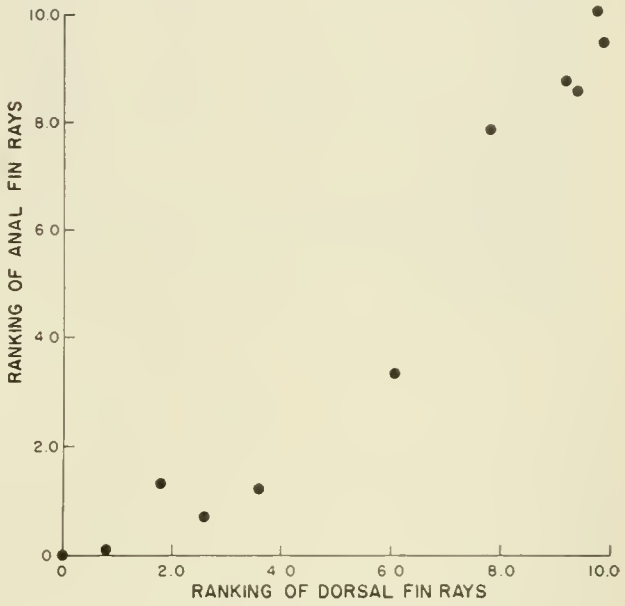

FIGURE 10.—Relation between dorsal and anal fin rays.

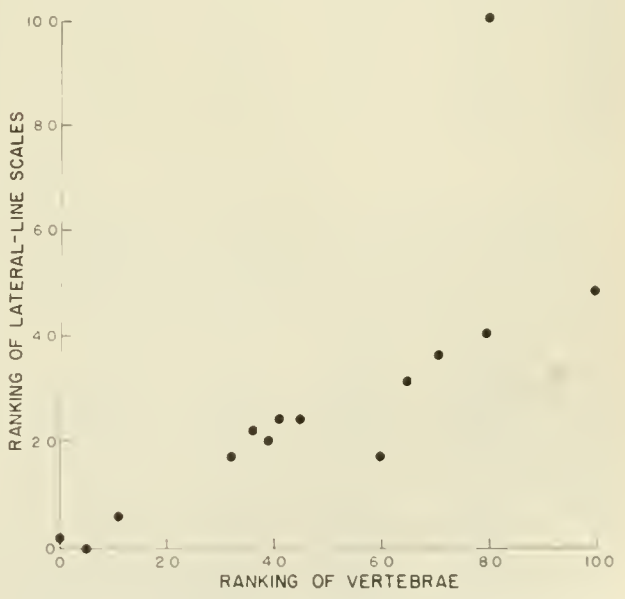

FIGURE 11.—Relation between vertebrae and lateral-line scales.

TABLE 26.—*Summary of ranking of means of meristic characters, by species*

Species	Branchiostegal rays	Pyloric caeca	Rays in—		Rakers on first gill arch	Vertebrae	Scales		
			Anal fin	Dorsal fin			On lateral line	Oblique rows	Dorsal fin to lateral line
Oncorhynchus:									
tshawytscha	10.0	7.5	10.0	9.9	3.4	10.0	4.8	2.5	4.4
gorbuscha	3.4	6.0	9.4	10.0	7.1	8.1	10.0	7.1	6.2
kisutch	5.7	2.7	7.8	7.9	2.8	6.5	3.1	1.4	2.3
keta	5.7	10.0	8.5	9.5	3.1	8.0	4.0	2.0	0.8
nerka	5.3	3.2	8.9	9.3	10.0	7.1	3.6	1.5	0.0
Cristivomer:									
namaycush	4.2	5.6	1.3	1.8	1.8	3.6	2.2	6.8	
Salmo:									
salar	2.8	1.6			1.5	0.5	0.0	0.0	
gairdneri		0.8	4.4		1.5	3.9	2.0	1.3	1.7
g. kamloops	2.2	1.2	3.5	6.1	1.3	[1] 4.1	2.4	2.5	
clarki		0.3				3.2	1.7	3.4	
trutta	0.0	0.7			0.0	0.0	0.2	0.8	
Salvelinus:									
alpinus	2.0	0.9	0.0	0.0	3.3	6.0	1.7	7.3	6.0
aureolus	1.1	1.0	0.1	0.8	0.9	4.1			
marstani	0.0	0.6	0.7	2.6	1.8	4.2			
oquassa	0.0								
malma	2.1	0.0		0.4	0.6	4.5	2.4	10.0	10.0
fontinalis	1.1	0.4	1.2	3.6	0.2	1.1	0.6	9.1	
Correlated characters:			11			13		8	
Number of paired entries									
Sum of ranks			51.4	61.5		[2] 58.5	[2] 28.7	33.1	31.4
Average rank			4.67	5.59		4.50	2.21	4.14	3.93
Average rank, both characters			5.13			3.35		4.03	
Correction factor [3]			1.10	.92		.74	1.52	0.97	1.03

[1] *g. whitehousei*=4.0.
[2] Exclusive of *garbuscha*.
[3] To put on a common basis.

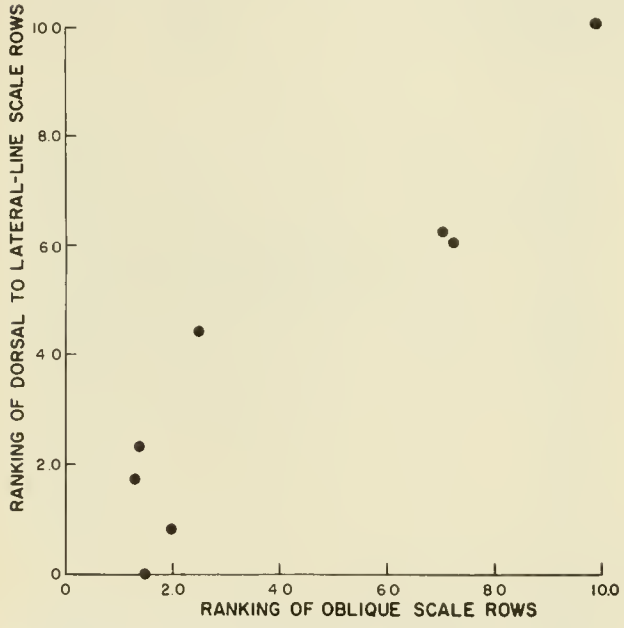

FIGURE 12.—Relation between oblique scale rows and scale rows from the dorsal to the lateral line.

Throughout the enumeration data there is a clear tendency for the variances to be correlated with their means. This tendency is easily seen in figures 4, 5, and 7, in which the 80 to 20 interpercentile range increases with an increase in the mean. This of course implies that the differences between mean rankings must be larger for higher rankings to be equally as significant as the smaller differences between mean rankings for lower rankings.

TABLE 27.—*Adjusted rankings of certain correlated meristic characters, by species*

I. Anal and dorsal fin rays

Species	Anal fin rays	Dorsal fin rays	Sum	Average rank
Oncorhynchus:				
tshawytscha	11.00	9.11	20.11	10.1
gorbuscha	10.34	9.20	19.54	9.8
kisutch	8.58	7.27	15.85	7.9
keta	9.35	8.74	18.09	9.0
nerka	9.79	8.56	18.35	9.2
Cristivomer:				
namaycush	1.43	1.66	3.09	1.5
Salmo:				
salar				
gairdneri	4.85		4.84	4.8
g. kamloaps	3.85	5.61	9.46	4.7
clarki				
trutta				
Salvelinus:				
alpinus	0.00	0.00	0.00	0.0
aureolus	0.11	0.74	0.85	0.4
marstoni	0.77	2.39	3.16	1.6
malma		0.37	0.37	0.4
fontinalis	1.32	3.31	4.63	2.3

II. Vertebrae and lateral-line scales

Species	Vertebrae	Lateral line scales	Sum	Average rank
Oncorhynchus:				
tshawytscha	7.40	7.30	14.70	7.4
gorbuscha	5.99	15.20	21.19	10.6
kisutch	4.81	4.71	9.52	4.8
keta	5.92	6.08	12.00	6.0
nerka	5.25	5.47	10.72	5.4
Cristivomer:				
namaycush	2.66	3.34	6.00	3.0
Salmo:				
salar	0.37	0.00	0.37	0.2
gairdneri	2.89	3.04	5.93	3.0
g. kamloops	3.03	3.65	6.68	3.3
clarki	2.37	2.58	4.95	2.5
trutta	0.00	0.30	0.30	0.2
Salvelinus:				
alpinus	4.44	2.58	7.02	3.5
aureolus	3.03		3.03	3.0
marstani	3.11		3.11	3.1
malma	3.33	3.65	6.98	3.5
fontinalis	0.81	0.91	1.72	0.9

TABLE 27.—*Adjusted rankings of certain correlated meristic characters, by species*—Continued

III. Oblique and dorsal-to-lateral-line scale rows

Species	Oblique rows	Dorsal to lateral rows	Sum	Average rank
Oncorhynchus:				
tshawytscha	2.42	4.53	6.95	3.5
gorbuscha	6.89	6.39	13.28	6.6
kisutch	1.36	2.37	3.73	1.9
keta	1.94	0.82	2.76	1.4
nerka	1.46	0.00	1.46	0.7
Cristivomer:				
namaycush	6.60		6.60	6.6
Salmo:				
salar	0.00		0.00	0.0
gairdneri	1.26	1.75	3.01	1.5
g. kamloops	2.42		2.42	2.4
clarki	3.30		3.30	3.3
trutta	0.78		0.78	0.8
Salvelinus:				
alpinus	7.08	6.18	13.26	6.6
malma	9.70	10.30	20.00	10.0
fontinalis	8.83		8.83	8.8

To correct for this correlation between the means and their variances, the adjusted rankings (table 28) were converted to logarithms. In order to avoid dealing with minus logarithms, and with the absence of any logarithm for a zero ranking, all rankings were first increased by 1 and then multiplied by 10. The logarithms of the rankings so derived are given in table 29.

One method of assessing the value of these meristic characters (table 29) is to determine whether the variation within each genus differs significantly from the variation between genera. Because the number of species varies from genus to genus, calculation of the variance must recognize unequal sample size (Snedecor, 1956: p. 268), considering each species as one sample mean.

TABLE 28.—*Adjusted rankings of meristic indices*

	Branchiostegals	Pyloric caeca	Anal and dorsal fin rays	Rakers on first gill arch	Vertebrae and lateral line scales	Oblique and dorsal-to-lateral-line scale rows
Species:						
Oncorhynchus:						
tshawytscha	10.0	7.5	10.1	3.4	7.4	3.5
gorbuscha	3.4	6.0	9.8	7.1	10.6	6.6
kisutch	5.7	2.7	7.9	2.8	4.8	1.9
keta	5.7	10.0	9.0	3.1	6.0	1.4
nerka	5.3	3.2	9.2	10.0	5.4	0.7
Cristivomer:						
namaycush	4.2	5.6	1.5	1.8	3.0	6.6
Salmo:						
salar	2.8	1.6		1.5	0.2	0.0
gairdneri		0.8	4.8	1.5	3.0	1.5
g. kamloops	2.2	1.2	4.7	1.3	3.3	2.4
clarki		0.3			2.5	3.3
trutta	0.0	0.7		0.0	0.2	0.8
Salvelinus:						
alpinus	2.0	0.9	0.0	3.3	3.5	6.6
aureolus	1.1	1.0	0.4	0.9	3.0	
marstoni	0.0	0.6	1.6	1.8	3.1	
malma	2.1	0.0	0.4	0.6	3.5	10.0
fontinalis	1.1	0.4	2.3	0.2	0.9	8.8
Genus:						
Oncorhynchus	6.02	5.88	9.20	5.28	6.81	2.82
Cristivomer	4.20	5.60	1.50	1.80	3.00	6.60
Salmo	1.67	0.92	4.75	1.08	1.84	1.60
Salvelinus	1.26	0.58	0.94	1.36	2.80	8.47

TABLE 29.—*Logarithm of adjusted rankings of meristic indices*

[Rankings: + 1 × 10]

	Branchiostegals	Pyloric caeca	Anal and dorsal fin rays	Rakers on first gill arch	Vertebrae and lateral line scales	Oblique and dorsal to lateral-line scale rows
Species:						
tshawytscha	2.04	1.93	2.05	1.64	1.92	1.65
gorbuscha	1.64	1.85	2.03	1.91	2.06	1.88
kisutch	1.83	1.57	2.00	1.60	1.76	1.46
keta	1.83	2.04	2.00	1.61	1.85	1.38
nerka	1.80	1.62	2.01	2.04	1.81	1.23
namaycush	1.72	1.82	1.40	1.45	1.60	1.88
salar	1.58	1.42		1.40	1.08	1.00
gairdneri		1.26	1.76	1.40	1.60	1.40
g. kamloops	1.51	1.34	1.76	1.36	1.63	1.53
clarki		1.11			1.54	1.63
trutta	1.00	1.23		1.00	1.08	1.26
alpinus	1.48	1.28	1.00	1.63	1.65	1.88
aureolus	1.32	1.30	1.15	1.28	1.60	
marstoni	1.00	1.20	1.41	1.45	1.61	
malma	1.49	1.00	1.15	1.20	1.65	2.04
fontinalis	1.32	1.15	1.52	1.08	1.28	1.99
Genus:						
Oncorhynchus	9.14	9.01	10.09	8.80	9.40	7.60
Cristivomer	1.72	1.82	1.40	1.45	1.60	1.88
Salmo	4.09(3)	6.36	3.52(2)	5.16(4)	6.93	6.82
Salvelinus	6.61	5.93	6.23	6.64	7.79	5.91(3)

The analysis of variance of the logarithms of the adjusted rankings of meristic characters follows:

Character index	Mean square		*F* value
	Between genera	Within genera	
Branchiostegals	0.2594	0.0438	5.92*
Pyloric caeca	.4210	.0229	18.38**
Anal and dorsal fin rays	.5255	.0203	25.89**
Rakers on first gill arch	.2171	.0421	5.16*
Vertebrae and lateral-line scales	.0430	.0808	.53
Oblique and dorsal to lateral-line scale counts	.2657	.0510	5.21*

For five of the six meristic indices, the variance within is significantly less than the variance between genera. This tends to confirm the validity of the generic groupings as established even though it does not yield much information concerning affiliations of particular species.

To show the relationships between species, both the maximum and the average differences in the logarithms of the six meristic indices are given for 16 species in table 30.

The interrelationships of the various species as shown by these meristic indices are depicted in figure 13. The genus *Oncorhynchus* is quite well separated from the other genera except for a close link between *O. kisutch* and *Salmo gairdneri*.

Cristivomer shows a loose affinity with *Salvelinus alpinus* and remote connections with several other species.

Salvelinus is a rather closely knit group, with *S. marstoni* the closest link between *Salmo gairdneri* and the other *Salvelinus*.

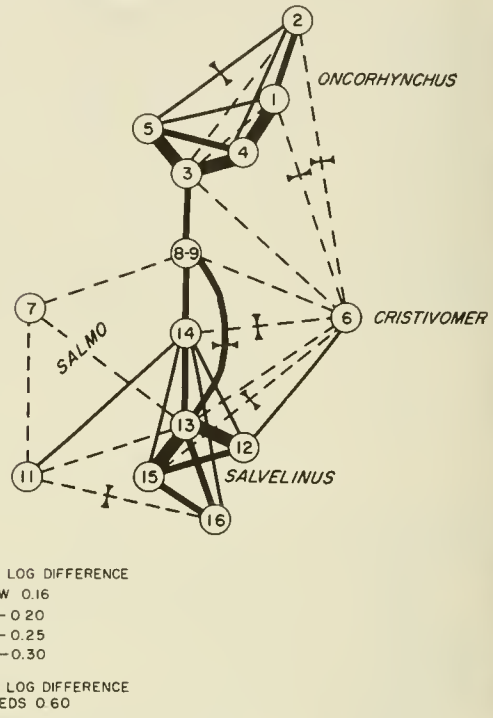

FIGURE 13.—Relationships of species of Salmonidae, as shown by meristic indices. (See table 30 for key to species' numbers in circles.

TABLE 30.—*Differences between logarithms of six meristic indexes, average differences between species (lower left), maximum differences (upper right)*

Species [1]	No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
tshawytscha	1		.40	.36	.27	.42	.65	.84	.67	.59	.82	1.04	1.05	.90	1.04	.93	.78
gorbuscha	2	.19		.42	.50	.65	.63	.98	.59	.55	.74	.98	1.03	.88	.65	.88	.83
kisutch	3	.26	.26		.47	.44	.60	.68	.31	.32	.46	.83	1.00	.85	.83	.85	.53
keta	4	.12	.24	.11		.43	.60	.77	.78	.70	.93	.83	1.00	.85	.84	1.04	.89
nerka	5	.25	.25	.14	.18		.65	.73	.64	.68	.51	1.04	1.01	.86	.80	.86	.96
namaycush	6	.30	.28	.28	.31	.39		.88	.56	.48	.71	.72	.54	.52	.72	.82	.67
salar (5)	7	.54	.57	.35	.45	.40	.40		.52	.55	.63	.58	.88	.52	.58	1.04	.99
gairdneri (5)	8	.35	.46	.19	.30	.33	.29	.27		.13	.23	.52	.76	.61	.35	.64	.59
g. kamloops	9	.35	.37	.20	.31	.33	.25	.25	.06		.23	.55	.76	.61	.51	.61	.46
clarki (3)	10	.41	.50	.28	.50	.39	.34	.45	.15	.14		.46	.25	.19	.09	.41	.36
trutta (5)	11	.72	.75	.53	.63	.60	.58	.29	.27	.36	.31		.63	.52	.53	.78	.73
alpinus	12	.46	.41	.37	.47	.48	.24	.38	.31	.25	.18	.47		.35	.48	.43	.55
aureolus (5)	13	.59	.57	.42	.54	.53	.27	.26	.19	.19	.22	.30	.15		.32	.30	.37
marstoni (5)	14	.58	.56	.40	.53	.53	.27	.34	.12	.22	.08	.25	.24	.17		.49	.37
malma	15	.58	.53	.48	.54	.60	.29	.46	.35	.28	.21	.45	.17	.12	.25		.37
fontinalis	16	.60	.54	.49	.60	.62	.33	.41	.32	.28	.22	.28	.31	.21	.24	.20	

[1] Figures in parentheses show number of comparisons when less than 6.

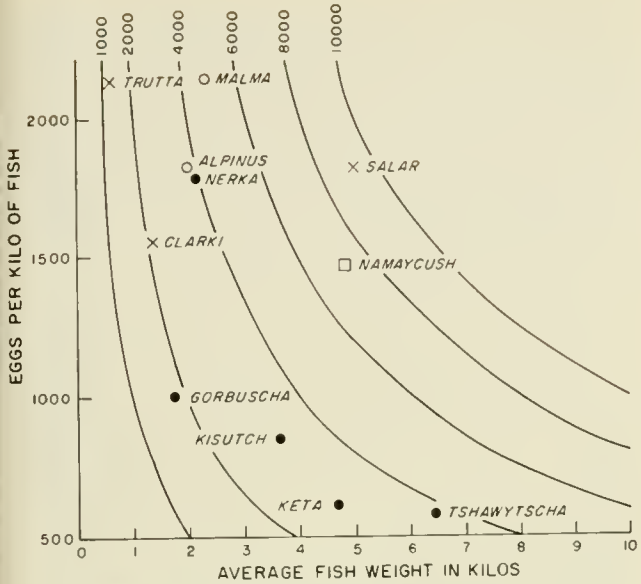

FIGURE 14.—Fecundity isopleths based on number of eggs per kilo of total weight versus the average weight of the adult fish.

The genus *Salmo* presents a very different picture. Of the three species, *salar*, *trutta*, and *gairdneri*, *S. trutta* shows connections with *Salvelinus marstoni*, only a remote affinity with *Salmo salar*, and none with *Salmo gairdneri*. *Salmo salar* shows equally remote associations with *Salmo trutta*, *Salvelinus aureolus*, and *Salmo gairdneri*. *Salmo gairdneri* is closely linked with *Oncorhynchus* (*kisutch*) on one hand and with *Salvelinus* (*marstoni*) on the other, and shows only a remote affinity with *Salmo salar* and none with *Salmo trutta*.

FECUNDITY

Although the term "fecundity" is normally used to denote the numbers of ova produced, we must also deal with the size of the ova. For each species of Salmonidae there is a normal range for both number and size of egg. For *Oncorhynchus*, which mature and spawn only once, this range is not too difficult to define. For species that live to spawn two or more times, the number of eggs varies widely, since the number is correlated with the weight of the fish (Rounsefell, 1957). Size of the egg is more constant for each species than the number, but tends to be larger in larger individuals.

Most of the available data on fecundity in the Salmonidae are given in some detail by Rounsefell (1957). From these data the average fecundity of the species for which data are available was plotted in figure 14. It will be noted at once that the lowest number of eggs per kilo of fish weight occurs in the fluvial anadromous *Oncorhynchus*. That this lower number of eggs per kilo of fish weight is not caused by a lower total weight of ova but rather to larger individual eggs is shown by figures 15 and 16, which show for available data the number of eggs per kilo of fish weight plotted against egg diameter and weight of fry, respectively.

Figures 15 and 16 show that the fluvial anadromous *Oncorhynchus* differ markedly in egg size from the other Salmonidae. The lacustrine anadromous *O. nerka* appears to be only slightly ahead of *S. salar* in egg size.

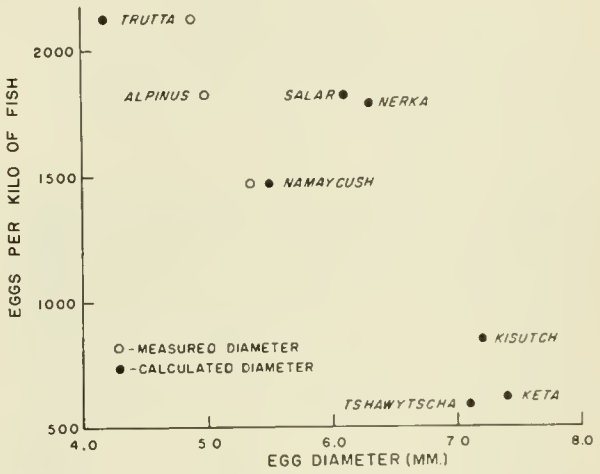

FIGURE 15.—Number of eggs per kilo of total weight versus the egg diameter.

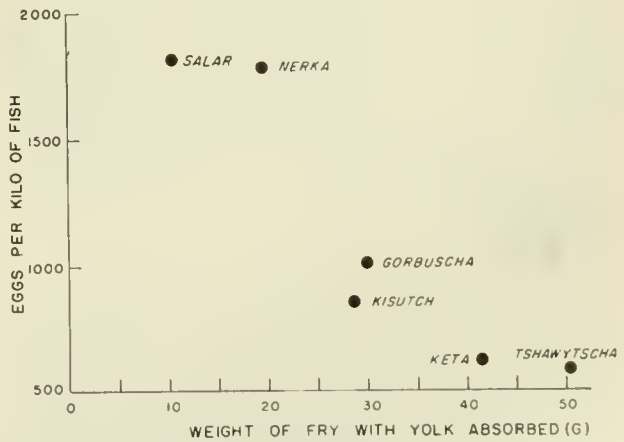

FIGURE 16.—Number of eggs per kilo of total weight versus the average weight of fry after absorption of the yolk.

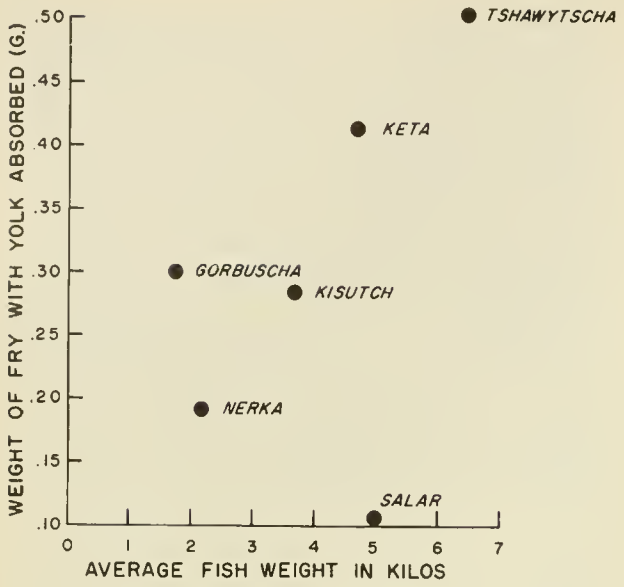

FIGURE 17.—Average weight of fry after absorption of the yolk compared with the average total weight of the species.

In considering egg size in relation to fish weight, however, it is obvious that *Oncorhynchus* can be distinguished even more clearly by this character. Thus, in figure 17, in which the weight of fry with the yolk absorbed is plotted against the average weight of the fish, *S. salar* has small fry for the size of the parent fish. In fact all five species of *Oncorhynchus* except *gorbuscha* fall in a straight line. The larger size of the fry (and of course the egg) of *gorbuscha* may be related to the extreme degree of anadromy in this species, whereby the fry emerge from the gravel as soon as the yolk is absorbed and migrate seaward at once.

DISTRIBUTION IN RELATION TO TEMPERATURE

Species may range over a wide area and yet avoid extreme conditions by changing spawning seasons and by occupying different ecological niches. A further complication is the tendency of isolated populations to change genetically. Despite these difficulties the overall picture shows that some of the species are definitely arctic or subarctic, whilst others range far to the south. The approximate latitudes given in table 31 are not too descriptive of the actual temperatures encountered because of the great differences in both sea-water and fresh-water temperatures at comparable latitudes on different coasts and the complicating factor of the lowering effect of altitude on fresh-water temperature.

TABLE 31.—*Limits of ranges of North American Salmonidae, ranked according to temperature of water frequented*

Species	Coldest water			Warmest water			Average cold rank	Final rank
	Locality	Latitude north	Cold rank	Locality	Latitude north	Cold rank		
alpinus	Ellesmere Island [1]	82°	1	Kodiak Island lakes	57°	4	2.5	1
namaycush	Banks Island [2]	73°	2	Lake Erie	41°	3	2.5	1
oquassa	Quebec lakes	50°	2	Lakes, northern Maine	45°	3	2.5	1
malma	Herschel Island [3]	71°	2	High streams, California	39°	4	3.0	2
keta	Cape Lisburne [4] MacKenzie River [5]	70°	2	Klamath River [6]	41°	5	3.5	3
gorbuscha	MacKenzie River [5]	70°	2	Russian R., California [7]	38°	5	3.5	3
nerka	Yukon River [8]	66°	3	Wallowa lakes, Oregon	45°	4	3.5	3
salar	Koksoak R., Ungava [9]	60°	2	Housatonic R., Connecticut	41°	6	4.0	4
fontinalis	Hudson Bay	59°	2	High streams, Georgia	35°	6	4.0	4
clarki	Southeast Alaska	60°	4	Eel River, California	39°	5	4.5	5
tshawytscha	Yukon River	66°	3	San Joaquin River	36°	7	5.0	6
kisutch	Norton Sound [10]	64°	3	Salinas R., California	36°	7	5.0	6
gairdneri	Kuskokwim R.	61°	3	Rio Presidio, Durango [11]	24°	8	5.5	7

[1] Fisheries Research Board (1959, p. 112).
[2] Fisheries Research Board (1959, p. 12).
[3] Scofield (1899).
[4] Bean (1882).
[5] Dymond (1940).
[6] Snyder (1931).
[7] Taft (1938).
[8] Evermann and Ooldsborough (1907).
[9] Dunbar and Hildebrand (1952).
[10] Nelson (1887).
[11] Needham and Gard (1959).

In order to obtain a picture of the effect of temperature on distribution, I have disregarded latitude in favor of generalized temperature isotherms. The mean surface ocean temperatures (see Davidson and Hutchinson, 1938) differ considerably at comparable latitudes on the eastern and western shores of the continent. In table 31, the water temperatures at the extreme ranges of the distribution have been ranked subjectively by species. This empirical method shows definite trends when the species are grouped according to their temperature distribution (averaging both extremes of the range).

The final rankings, by species and genus, according to distribution in cold waters, are as follows:

Rank and species	*Cristivomer*	*Salvelinus*	*Oncorhynchus*	*Salmo*
Rank 1:				
namaycush	X			
alpinus		X		
oquassa		X		
Rank 2:				
malma		X		
Rank 3:				
keta			X	
gorbuscha			X	
nerka			X	
Rank 4:				
fontinalis		X		
salar				X
Rank 5:				
clarki				X
Rank 6:				
tshawytscha			X	
kisutch			X	
Rank 7:				
gairdneri				X
Rank by genus	1	2	4.2	5.3

Cristivomer and *Salvelinus* are arctic and subarctic genera, except that *S. fontinalis*, which differs most widely from the other species of *Salvelinus* in respect to other characteristics is more southerly. All *Oncorhynchus* species range far to the north, but *tshawytscha* and *kisutch* are more tolerant than the others of warmer water. *Salmo salar* lives in colder water than either of the Pacific species of *Salmo*. The range of *clarki* is peculiar in that it extends neither far to the north nor far to the south, but inhabits the temperate waters between. While it extends to Bristol Bay, *gairdneri* avoids the colder streams and extends into much warmer waters than any of the other species.

COMPARISON OF NORTH AMERICAN AND ASIATIC GENERA

Some authors classify the salmons and trouts, together with the graylings and whitefishes, in a single family, which they call Salmonidae. We prefer to consider them as three families, the Thymallidae, Coregonidae, and Salmonidae. The last is the group discussed below.

In addition to the genera of Salmonidae that occur in North America two fresh-water genera occur only in Asia (Dymond and Vladykov, 1934). *Brachymystax* occurs across Siberia and south to the rivers of Japan and the Okhotsk Sea. *Hucho* consists of three species, one on the Danube, one in the rivers of Siberia, and a third in Sakhalin and the rivers entering the Okhotsk Sea (Dymond and Vladykov, 1934).

Some notion of the relationship between these two purely Asiatic genera and the other four genera is obtained by comparing their osteology since other characteristics are not sufficiently well-documented for the Asiatic genera. Furthermore, morphological material is chiefly available for only one or two species of each genus. The available osteological data are well summarized by Norden (1958). As Norden classed *Cristivomer* under *Salvelinus* and used *Cristivomer namaycush* as his chief representative of *Salvelinus*, we are forced to combine these two genera for the purpose of this comparison (table 32).

TABLE 32.—*Comparison of certain generic characteristics in Salmonidae*

[Osteological characters adapted from Norden, 1958]

Character	*Brachymystax*	*Hucho*	*Salvelinus-Cristivomer*	*Salmo*	*Oncorhynchus*
Mouth:					
Small	A				
Large		B	B	B	B
Jaw hinge:					
Below orbit	C				
Behind orbit		D	D	D	D
Palatine and vomerine teeth:					
In continuous U-shaped band	E	E			
Narrowly separated			F	F	
Widely separated					G
Ova:					
Small	H				
Medium		I	I		
Large				J	
Very large					K
Jaw teeth:					
Small, fine	L				
Strong		M	M	M	M
Shaft of vomer:					
Short, toothless	N	N			
Long, toothless			O		
Long, toothed				P	P
Postorbitals contact preopercle:					
No	Q	Q	Q	Q	
Yes					R
Dorsal fontanelles:					
Persistent	S	S	S	S	
Covered in adult					T
Supraethmoid:					
Long and narrow with posterior projections	U	U	U		
Short, notched posteriorly				V	V
Ascending process of premaxilla:					
Intermediate in size	W	W		W	
Well-developed			X		
Absent in adults					Y

The number of differences between genera in ten characters (from table 32) are summarized in table 33.

The relationships between genera based only on the 10 characters of table 32 are depicted in figure 18, in which the distances between genera are roughly proportional to the number of differences in characters (from table 33).

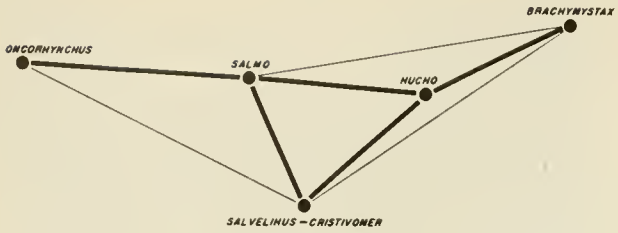

FIGURE 18.—Diagrammatic comparison of genera based on certain characters.

It appears that *Brachymystax* is the most primitive and generalized of the genera, *Hucho* represents an intermediate stage, whilst *Oncorhynchus* is the most specialized.

TABLE 33.—*Number of certain characters differing between genera of Salmonidae*

[Characters from table 32]

	Brachymystax	*Hucho*	*Salvelinus-Cristivomer*	*Salmo*	*Oncorhynchus*
Brachymystax		4	7	7	10
Hucho	4		3	4	7
Salvelinus-Cristivomer	7	3		4	7
Salmo	7	4	4		5
Oncorhynchus	10	7	7	5	

SUMMARY OF RELATIONSHIPS

The foregoing material on hybridization, coloration, anadromy, fecundity, morphological characters, et cetera, show the relationships between the

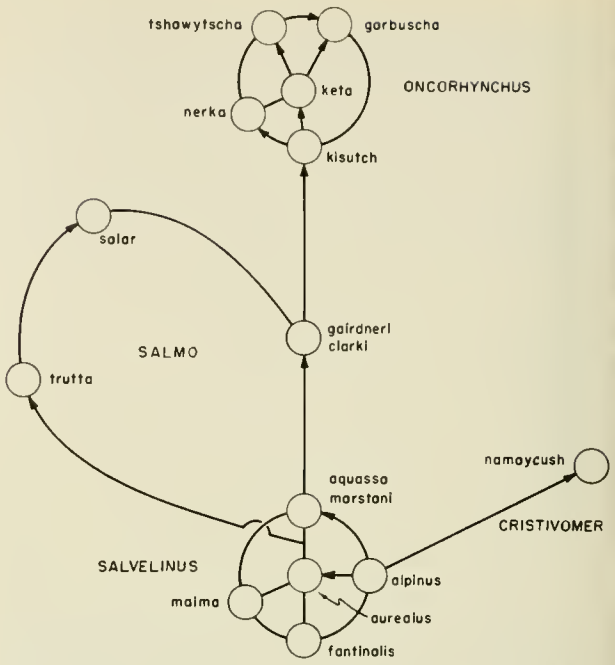

FIGURE 19.—Suggested relationships among North American Salmonidae.

North American species of Salmonidae. In figure 19 the degrees of relationship have been indicated by the relative distances between species. Since many of the differences and similarities are difficult to weigh with the information presently available concerning the relative value of different criteria, I have not attempted to be more precise.

ANNOTATED KEY TO NORTH AMERICAN SALMONIDAE

This annotated key is given in place of the more conventional strictly dichotomous key. Keys are used chiefly to determine the identity of a specimen, and each subdivision should not be interpreted as denoting relationships.

The amount of information available varies widely from species to species, but where available, certain items (such as chromosome number) have been included. Thus, although this section has been arranged as a key, it is also a summarized description of the North American Salmonidae. It should be kept in mind that this paper is based wholly on published data and that no attempt was made to verify points that await further study.

KEY TO GENERA

A. Skeleton cartilaginous, very slight calcification; dorsal fontanelles closed in adults; postorbitals contact preopercle; ascending process of premaxilla absent in adults; branchiostegal rays (left side) 10–19; gill rakers (first arch, left side) 19–39; lateral-line scales 121–198; anal fin rays 15–22; pyloric caeca 55–249; dorsal fin rays 12–18; vertebrae 62–75; only black spots or speckling at all ages (except breeding colors); ova and fry very large in relation to adult size; anadromy obligatory or adaptive; mouth lining dark to black; all adults die after spawning.
Genus *ONCORHYNCHUS*, Pacific salmons.

AA. Skeleton fairly well calcified; dorsal fontanelles persistent; postorbitals do not contact preopercle; ascending process of premaxilla persistent; branchiostegal rays (left side) 8–14; gill rakers (first arch, left side) 14–27; lateral-line scales 105–138; anal fin rays 8–16; pyloric caeca 20–170; dorsal fin rays 9–15; vertebrae 57–69; light spots, speckling, or colored areas present at some stage; ova and fry medium to small in relation to adult size; anadromy not adaptive or obligatory; mouth lining white to black; some adults may die after spawning.

B. Teeth on both head and shaft of vomer; supraethmoid short, width medium to broad, notched posteriorly; lateral-line scales 105–138; anal fin rays 9–16; all have black body spots or speckling but may also have light spots or areas at some stages; fins without conspicuous white leading edge.

Genus *SALMO*, Atlantic salmons and trouts.

BB. Teeth on head (anterior end) of vomer only; supraethmoid long, narrow, with posterior projections; lateral-line scales 109–131; anal fin rays 8–12; body spots yellow to red or gray, never black; no lateral body stripe; white leading edge on paired fins.

C. Basibranchial (hyoid) teeth numerous and strong; supralingual (tongue) teeth in parallel rows; pyloric caeca 95–179 (average about 127–138); caudal fin deeply forked; pearl organs in adults; no bright colors, but spotted with gray; egg diameter less than 5.0 mm.; lacustrine; diploid chromosome number 84.

Genus *CRISTIVOMER*, lake trouts.

CC. Basibranchial (hyoid) teeth few or missing, weak; supralingual (tongue) teeth form equal sides of an isosceles triangle; pyloric caeca 20–64 (average about 28–46, 30–99 in *S. aureolus*); caudal fin very little to deeply forked; no pearl organs; brightly colored in fresh water, spotted with yellow, pink, or red, lower fins usually brightly colored; egg diameter usually more than 5.0 mm.; adfluvial, fluvial, or optionally anadromous.

Genus *SALVELINUS*, charrs.

KEY TO SPECIES

Salvelinus. Charrs

A. Basibranchial (hyoid) teeth absent or rare; back with dark wavy "wormlike" vermiculations extending onto dorsal fin; lower fins with white front edge followed by a black stripe; tip of lower jaw black; some of lateral spots may be pink or red with a blue halo; roof of mouth black; end of caudal fin almost square in adults; anal fin falcate; diploid chromosome number 84; optionally anadromous, fluvial, or adfluvial; very short migrations in the sea ..... *Salvelinus fontinalis*, Speckled charr or eastern charr (eastern brook trout).

AA. Basibranchial (hyoid) teeth usually present, weak to moderate; vermiculations on back absent or faint; no black stripe on lower fins; tip of lower jaw white to reddish; lateral spots without blue borders; caudal fin slightly to well-forked in adults; optionally anadromous, adfluvial, or lacustrine.

B. Pyloric caeca 20–39 (average about 28–29); numerous red dots on sides (+50) smaller than diameter of pupil; pectoral fins very seldom if ever with white anterior margin; caudal fin almost square in adults; optionally anadromous or fluvial; short migrations in the sea ..... *Salvelinus malma*, dolly varden charr.

BB. Pyloric caeca 20–99 (average about 38–46); spots on sides orange; all lower fins with white anterior margin; caudal fin well-forked; optionally anadromous, adfluvial, or lacustrine.

C. Maxillary extending about to posterior margin of eye; lateral spots (orange or yellowish) very small and numerous; roof of mouth white; white margin of lower fins narrow; adfluvial.

Salvelinus oquassa, blueback charr.

Salvelinus o. marsloni, red Quebec charr.

CC. Maxillary extending well beyond posterior margin of eye; orange or yellowish lateral spots small to large; broad white anterior edge on lower fins, roof of mouth white to blackish; optionally anadromous or adfluvial; short migrations in the sea (*alpinus*) ..... *Salvelinus alpinus*, Arctic charr.

Salvelinus a. aureolus, golden charr or Sunapee charr.

Salmo. Salmons and trouts

A. Parr with small orange blotches or spots on sides adjacent to lateral line; black spots on caudal fin absent or few; adults may have pink or blue halo surrounding black spots on body; adult *S. salar sebago* may have some colored spots; caudal peduncle stout or slender, anal fin rays 9–11 (complete count).

B. Teeth on head and shaft of vomer strong and well-developed; branchiostegal rays average 10.0; oblique scale rows 116–136; end of maxillary usually not far behind posterior margin of eye; large black spots on body with some often surrounded by pink or red halo; few smaller reddish spots adjacent to lateral line; orange blotch on adipose usually present even in sea-run individuals, no colored lateral band; tail never deeply forked, square to fan-shaped in older fish; tail unspotted; caudal peduncle stout; diploid chromosome number 80; optionally anadromous, fluvial, or adfluvial; short migrations in the sea ..... *Salmo trutta*, brown trout.

BB. Teeth on vomer all short, weak; branchiostegal rays average 11.9; oblique scale rows 111–118; maxillary extending to or slightly behind posterior margin of eye; small black spots, often x-shaped, numerous on upper body, sometimes extending slightly onto dorsal, adipose, and anal fins; landlocked varieties may have some lighter spots on body; caudal peduncle slender; no colored lateral band; caudal usually without spots, caudal slightly to well-forked in adults; some adults die after spawning; diploid chromosome number 60; optionally anadromous or adfluvial; long migrations in the sea; not abundant far offshore ..... *Salmo salar*, Atlantic salmon.

Salmo s. sebago, landlocked salmon.

AA. Parr with bright lateral band, usually reddish or iridescent; black spots on back, and on dorsal, adipose, and caudal fins; adults without colored spots; caudal peduncle stout, and anal fin rays 11–16 (complete count).

C. Usually with red streak on underside of lower jaw which may be concealed by mandible; maxillary extends well beyond posterior margin of eye; oblique scale rows 122–208; pyloric caeca 27–40; in breeding color, belly suffused with red, lower fins reddish; adults seldom with a red lateral band; mouth lining white; optionally anadromous, fluvial, or adfluvial; very short migrations in the sea.

Salmo clarki, steelhead cutthroat trout or cutthroat trout.

CC. No red streak under jaw, maxillary extends to or slightly beyond posterior margin of eye; oblique scale rows 115–164; pyloric caeca 25–61 (average about 47); wide pink or red lateral band, especially bright in spawning males; mouth lining white; some sea-run adults die after spawning; optionally anadromous, fluvial, or adfluvial; chiefly coastwise migrations at sea---- *Salmo gairdneri*, steelhead rainbow trout or rainbow trout.

Salmo g. kamloops, Kamloops trout.

Oncorhynchus. Pacific salmons

A. Lateral-line scales 160–198 (average about 184); branchiostegals 9–15; pyloric caeca 95–224 (average about 136); anal rays 16–20 (complete count); gill rakers 24–34 (average about 29.7) with minute teeth; large black spots tending to oval on back and on entire caudal fin; young without parr marks; mouth lining dark; very pronounced hump on breeding males; mature at 2 years of age; obligatory anadromous; long sea migrations; abundant far offshore; usually less than 2,000 ova---------- *Oncorhynchus gorbuscha*, pink salmon.

AA. Lateral-line scales 124–165; branchiostegals 10–19; pyloric caeca 45–254; anal rays 15–22 (complete count); gill rakers 19–39; no black spots on lower lobe of caudal fin, may be black speckling on dorsal edge of upper lobe; young with distinct parr marks; mature normally at ages 3–8, usually more than 2,500 ova.

B. Pyloric caeca 85–254; lateral-line scales 130–165; branchiostegals 10–19; anal rays 16–22 (complete count); gill rakers 19–28.

C. Lateral-line scales 130–147 (average about 139); branchiostegals 10–16; pyloric caeca 140–254 (average about 205); anal rays 16–20 (complete count); gill rakers 19–26 (average about 22), rakers wide apart and without teeth; caudal peduncle slender; parr marks short, elliptical or oval, extending little, if any, below lateral line; no black speckling on back or fins; breeding color anterior two-thirds of sides with bold jagged reddish line, posterior third of sides with jagged black line; mouth lining dark; obligatory anadromous, long sea migrations, abundant far offshore---------- *Oncorhynchus keta*, chum salmon.

CC. Lateral-line scales 130–165 (average about 146); branchiostegals 13–19; pyloric caeca 85–244 (average about 158); anal rays 16–22 (complete count); gill rakers 20–28 (average about 24), rakers wide apart with large teeth; caudal peduncle stout; parr marks large vertical bars almost bisected by lateral line; small black speckling on back, dorsal fin, and upper lobe of caudal fin, sometimes extending onto adipose fin and lower lobe of caudal and faintly onto anal fin; breeding adults without red on sides; mouth lining black; obligatory anadromous; long sea migrations; not abundant far offshore------ *Oncorhynchus tshawytscha*, king salmon.

BB. Pyloric caeca 45–114; lateral-line scales 124–150; branchiostegals 11–16; anal rays 15–21 (complete count); gill rakers 19–39.

D. Pyloric caeca 45–114 (average about 75); lateral-line scales 130–144 (average about 135); branchiostegals 11–15; anal rays 15–19 (complete count); gill rakers 19–25 (average about 21), rakers wide apart with large teeth, none on back of second and fourth gill arches; caudal peduncle stout; parr marks large vertical bars almost bisected by lateral line; anal fin of parr falcate with first ray whitish; other lower fins of parr orange-tinged and white-tipped; in adults black speckling on back, often extending along upper edge of caudal fin and base of dorsal fin; sides of breeding adults may be suffused with light pink, but no definite markings; mouth lining dark; adaptively anadromous; long sea migrations; not abundant far offshore.

Oncorhynchus kisutch, silver salmon.

DD. Pyloric caeca 45–114 (average about 86); lateral-line scales 124–150 (average about 135); branchiostegals 11–16; anal rays 15–21 (complete count); gill rakers 28–39 (average about 35), rakers close together with minute teeth and present on back of second and fourth gill arches; caudal peduncle slender; parr marks short, elliptical or oval, extending little, if any, below lateral line; black speckling, when present, is faint, fins without speckling, except faint speckling on margin of caudal in breeding fish; in breeding adults, body (except lower belly) and all fins except pectorals and caudal lobes a deep crimson to brick red, head a dull green on dorsal half, creamy white below; mouth lining dark; adaptively anadromous; long sea migrations; abundant far offshore---------- *Oncorhynchus nerka*, sockeye salmon.

Oncorhynchus n. kennerlyi, kokanee.

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APPENDIX

The scientific names mentioned in text, tables, or footnotes with their English equivalents are listed below. The preferred common name is marked with an asterisk.

SALMONIDAE. SALMONS, TROUTS, and CHARRS

Salvelinus, CHARRS	
alpinus	Arctic charr*, alpine charr, red lake charr
aureolus (or *alpinus aureolus*)	Golden charr*, Sunapee charr
fontinalis	Eastern charr*, speckled charr, eastern brook trout
malma	Dolly varden*, dolly varden charr
marstoni (or *oquassa marstoni*)	Red Quebec charr
oquassa	Blueback charr
Cristivomer, LAKE TROUTS or LAKE CHARRS	
namaycush	Lake trout*, lake charr, togue, namaycush
Salmo, SALMONS and TROUTS	
clarki	Cutthroat trout*, cutthroat steelhead*
clarki lewisi	Black-spotted trout*, Yellowstone trout
clarki pleuriticus	Cutthroat trout*, Colorado River trout
clarki seleniris	Piute trout
gairdneri	Rainbow trout*, rainbow steelhead*
gairdneri agua-bonita	Golden trout
gairdneri kamloops	Kamloops trout
gairdneri whitehousei	Mountain rainbow
salar	Atlantic salmon
salar sebago	Landlocked salmon*, ouaniche, Sebago salmon
trutta	Brown trout, sea trout
trutta trutta	Sea trout*, Loch Leven trout
trutta fario	Brown trout
Oncorhynchus, PACIFIC SALMONS	
gorbuscha	Pink salmon*, humpback salmon
keta	Chum salmon*, dog salmon
kisutch	Silver salmon, coho (Alaska), silverside (Columbia River)
nerka	Sockeye salmon, red salmon (Alaska), blueback (Columbia River)
nerka kennerlyi	Kokanee*, silver trout (Washington), little redfish
tshawytscha	King salmon, spring salmon (British Columbia), chinook (Northwest), tyee
masou	Masu salmon

MIDWATER TRAWLING FOR FORAGE ORGANISMS IN THE CENTRAL PACIFIC, 1951–1956

By Joseph E. King and Robert T. B. Iversen, *Fishery Research Biologists*
Bureau of Commercial Fisheries

Since the inauguration of field work early in 1950, the staff of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu,[1] has conducted studies on the oceanography, productivity, and fishery resources of the central Pacific Ocean. Although not a major activity of the Laboratory's research program, midwater trawling has received considerable attention. Four kinds of trawls were tested and employed to a varying extent on 22 cruises in the central Pacific from 1951 to 1956. Trawling was not conducted, however, with the expectation of discovering new fishery resources of commercial importance, but rather to sample quantitatively the forage organisms which are the basis and support of fishery stocks in general, and particularly those organisms utilized by the tunas.

Midwater trawling has been conducted along the west coasts of Canada and the United States by a number of institutions employing different types of gear. The Fisheries Research Board of Canada, Biological Station, Nanaimo, British Columbia, pioneered in the development of a commercial-type trawl for use in the herring fishery (Barraclough and Johnson, 1956). This trawl, or one of its modifications, has been used by the Bureau of Commercial Fisheries in fishery explorations in the eastern Pacific (U.S. Fish and Wildlife Service, 1956; Schaefers and Powell, 1958). The California Department of Fish and Game has also tested a commercial-type midwater trawl of somewhat different design (Pacific Fisherman, 1953). The Isaacs-Kidd midwater trawl was developed at Scripps Institution of Oceanography to collect bathypelagic fishes and invertebrates (Devereaux and Winsett, 1953). This type of trawl has been employed by Scripps staff members on numerous cruises in the eastern Pacific and has also been used recently in the northeastern Pacific by personnel of the University of Washington Department of Oceanography to relate variations in the abundance of plankton and nekton to other oceanographic features (Aron, 1959). Some of the studies mentioned here have resulted in discoveries and information that have been of great value and interest to the commercial fishing industry, and all have made worthwhile contributions to our scant knowledge of the abundance and distribution of animal life in the mid-depths of the ocean—a life zone that presently contributes little in the way of human food (Whiteleather, 1957; Powell, 1958).

Specific objectives of the trawling program were as follows:

(1) To obtain a measure of the abundance and distribution of potential tuna food; (2) to obtain an estimate of the standing crop of forage organisms; (3) to sample juvenile tunas; (4) to learn something of tuna feeding behavior, e.g., depth of feeding, diurnal variation, and selectivity; and (5) to evaluate the general catching abilities of different midwater trawls in the highly transparent waters of the tropical and subtropical Pacific. This report describes and evaluates the results of our trawling studies with respect to these objectives.

H. J. Mann, of the Honolulu laboratory, prepared the engineer's drawings of the trawls and helped the authors with the detailed descriptions of the trawls. From the engineer's drawings, Tamotsu Nakata prepared the drawings and other figures that appear in this paper. Isaac Ikehara and Allen Shimomura assisted in the sorting, counting, volume measurement, and identification of the organisms in the collections.

[1] Formerly Pacific Oceanic Fishery Investigations.

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TABLE 1.—*Number of hauls, cruises, and general areas where midwater trawling was accomplished, by type of gear, central Pacific, 1951–56*

Gear and cruise	Cruise period	General area	Number of hauls
6-foot beam trawl:			
John R. Manning: Cruise 9	November 1951	Hawaiian waters	10
Hugh M. Smith:			
Cruise 14	February 1952	Equatorial Pacific	2
Cruise 15	June 1952	do	4
Subtotal			16
1-meter ring trawl:			
Charles H. Gilbert:			
Cruise 11	April 1953	Hawaiian waters	10
Cruise 12	May 1953	do	10
Cruise 13	June 1953	do	2
Hugh M. Smith: Cruise 21	August 1953	do	1
Subtotal			23
6-foot Isaacs-Kidd trawl:			
John R. Monning:			
Cruise 15	May 1953	Equatorial Pacific	1
Cruise 16	July 1953	do	3
Cruise 20	April-May, 1954	Equatorial Pacific and Hawaiian waters	22
Cruise 21	July 1954	Hawaiian waters	4
Cruise 22	September–October, 1954	North Pacific and Hawaiian waters	10
Cruise 23	December 1954	North Pacific	2
Cruise 24	March–April 1955	Equatorial Pacific	13
Hugh M. Smith: Cruise 27	January–February, 1955	North Pacific and Hawaiian waters	23
Subtotal			78
10-foot Isaacs-Kidd trawl:			
Hugh M. Smith:			
Cruise 27	January–February, 1955	North Pacific	3
Cruise 30	July–August, 1955	North Pacific and Hawaiian waters	37
Cruise 31	September–December, 1955	Equatorial Pacific	53
Cruise 32	February 1956	Hawaiian waters	8
Cruise 33	March 1956	Equatorial Pacific	5
Cruise 34	May 1956	Hawaiian waters	4
Cruise 35	August–October, 1956	Equatorial Pacific and Hawaiian waters	43
Cruise 37	December 1956	Enlwetok	4
Subtotal			157
Total			274

SOURCE OF DATA

This report is concerned with the results of 274 midwater trawl hauls made on 22 cruises of Bureau of Commercial Fisheries vessels in the central Pacific during the years 1951–56. A summary of the hauls made and the general areas sampled by each vessel on each cruise is given in table 1. Positions of the trawl stations are supplied in appendix tables 1 to 4.

The area investigated extended from latitude 49° N. to 19° S. and from longitude 108° W. to 162° E. The approximate positions of stations where each type of trawl was employed are shown in figures 1 to 4.

DESCRIPTION OF GEAR AND METHODS OF HAULING

This report is concerned with the results obtained with four kinds of trawls: (1) 6-foot beam trawl, (2) 1-meter ring trawl, (3) 6-foot Isaacs-Kidd trawl, and (4) 10-foot Isaacs-Kidd trawl. A description of each trawl follows.

6-FOOT BEAM TRAWL

This trawl consists of a net 30 feet in length with a 6-foot-square mouth opening held open across the top and bottom by 6-foot lengths of galvanized pipe (fig. 5). The body of the net is constructed of 1-inch (stretched measure) cotton netting; the cod end is of ½-inch mesh. The rear half of the net, including the cod end, is lined with 3/16 mesh (square measure) minnow netting. We do not know where the design for this gear originated.

This trawl was operated from the *John R. Manning* and the *Hugh M. Smith* at speeds of 4 to 5 knots, using a towing cable of ¼-inch wire rope. On each haul a 50-pound bronze depressor or a 100-pound streamlined lead weight was suspended from the lower pipe beam. Table 2 gives the minimum and maximum towing tensions obtained when hauling at various speeds and with different amounts of wire out. At the usual hauling speed (4 to 5 knots) the maximum tension did not exceed 2,000 pounds. Most hauls were oblique tows, ranging from the surface to depths as great as 450 meters. The depth of the haul was esti-

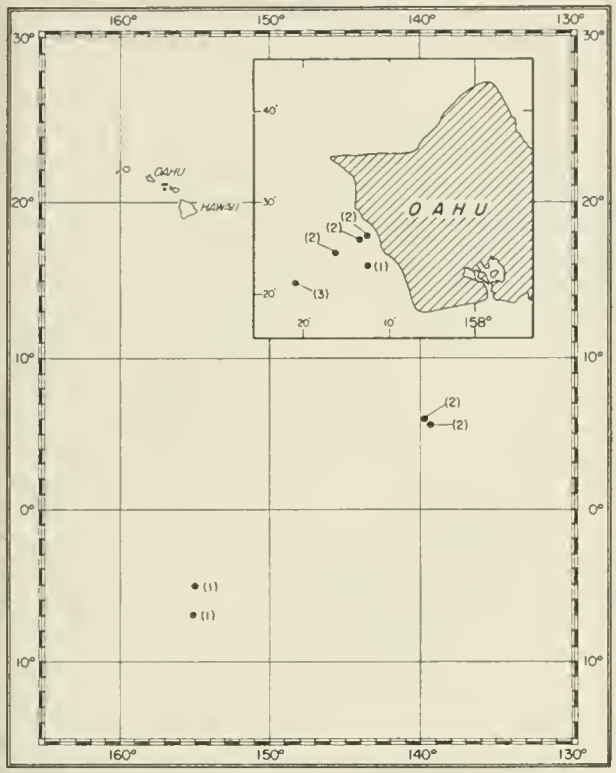

FIGURE 1.—Location of the 16 stations where hauls were made with the 6-foot beam trawl. (Number of stations in parentheses.)

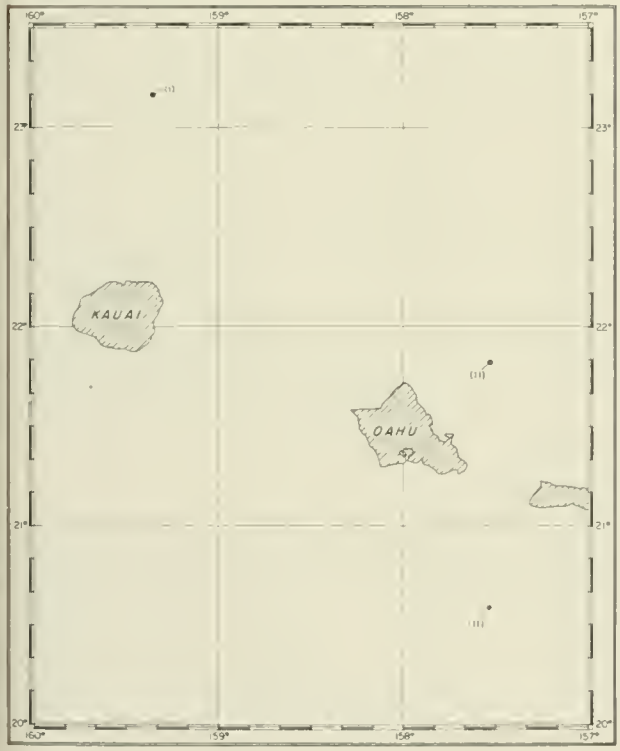

FIGURE 2.—Location of the 23 stations where hauls were made with the 1-meter ring trawl. (Number of stations in parentheses.)

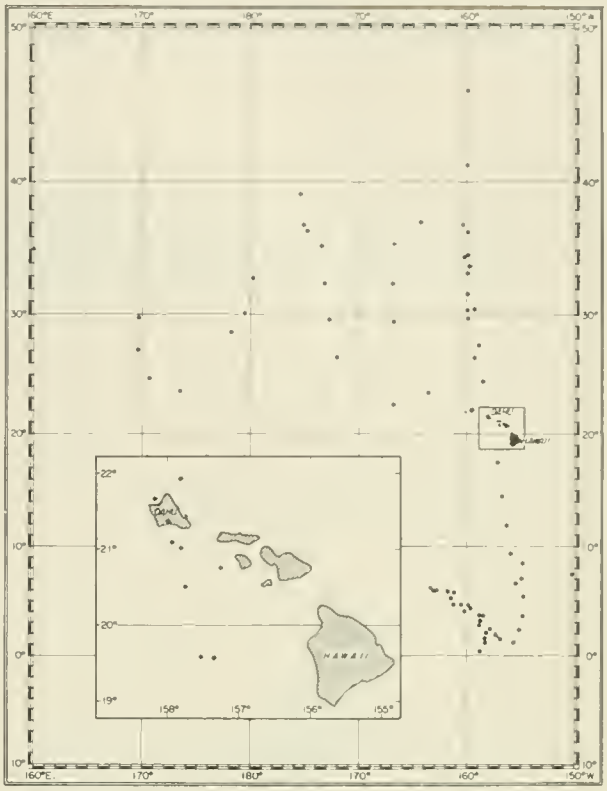

FIGURE 3.—Location of the 78 stations where hauls were made with the 6-foot Isaacs-Kidd trawl.

mated from the angle of the towing wire and the length of wire out, using the secant relationship with the assumption that the towing wire described a straight line in the water.

TABLE 2.—*Towing tensions obtained with the 6-foot beam trawl, measured with a dynamometer, on* John R. Manning *cruise 9*

Wire out	Main engine speed	Estimated vessel speed	Towing tension	
			Minimum	Maximum
	R.p.m.	*Knots*	*Pounds*	*Pounds*
10 meters	110	3.5	430	640
10 meters	150	4.7	850	1,280
200 meters	150	4.7	850	1,280
400 meters	150	4.7	920	1,350
400 meters	200	6.2	1,280	2,200

The collections were stored in glass jars and preserved in formalin neutralized with borax.

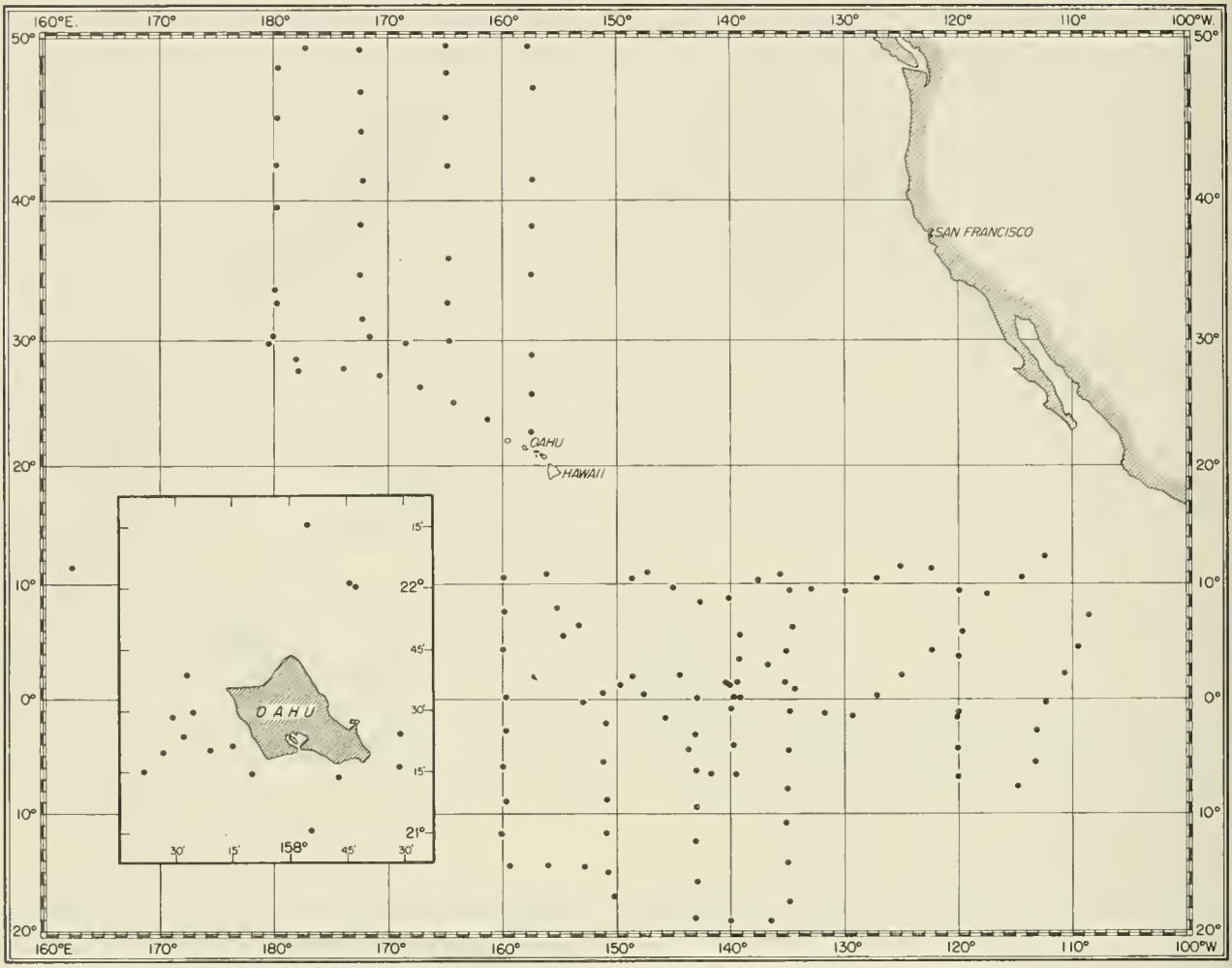

FIGURE 4.—Location of the 157 stations where hauls were made with the 10-foot Isaacs-Kidd trawl.

1-METER RING TRAWL

This gear, which we termed a "ring trawl," consists of a circular net, 1-meter in mouth diameter and 4½ meters in length, attached to a steel ring 1-meter in diameter (fig. 6). The net is of 2-inch mesh (stretched measure) No. 12 cotton twine and is equipped with a cod-end liner of 3/16-inch mesh (square measure) minnow netting. On most hauls an additional liner, slightly more than 1 meter in length and of ½-inch mesh (stretched measure) cotton netting, was attached in the net just forward of the cod end.

Except for one haul this gear was operated only from the *Charles H. Gilbert*, usually at speeds of 6 to 7 knots, but reaching a maximum of 8½ knots on a few test hauls. The towing cable was ¼-inch diameter wire rope. The 1-meter ring at the mouth of the net was initially constructed of ⅞-inch stock and was without reinforcement. At higher towing speeds the ring did not retain its shape and was replaced with one of 1-inch thickness, reinforced with two transverse bars (fig. 6).

A 50-pound depressor or a 100-pound streamlined weight was suspended below the net. At average towing speeds (6 to 7 knots), the maximum towing tension did not exceed 1,000 pounds (table 3). The trawl was operated, usually on oblique tows, at depths ranging from the surface to 200 meters. As in the case of the 6-foot beam trawl, the depth of haul was calculated trigono-

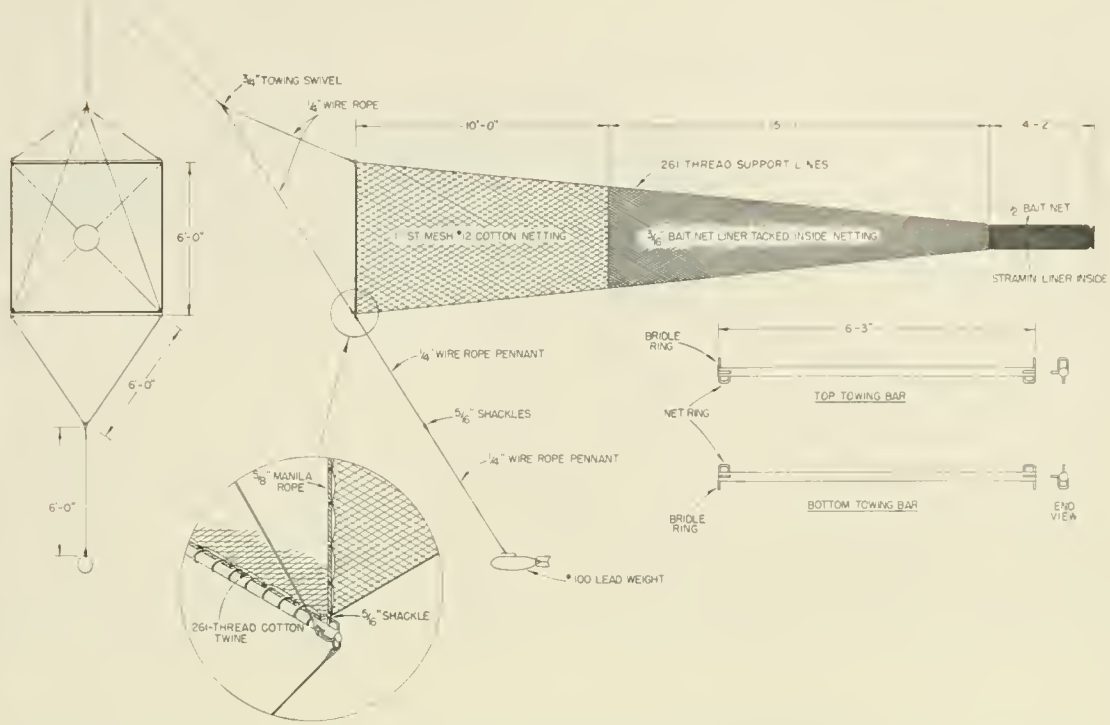

FIGURE 5.—Diagram of the 6-foot beam trawl, showing the arrangement of weight and bridle lines.

metrically with the assumption that the towing wire described a straight line.

6-FOOT ISAACS-KIDD TRAWL

A scaled down, 6-foot model of the Isaacs-Kidd trawl was constructed from plans provided by Scripps Institution of Oceanography for 10- and 15-foot models. The net is 28 feet in length with the forward section of 1½-inch mesh (stretched measure) No. 9 cotton twine; the middle section is of ¾-inch mesh and the rear section of ½-inch mesh (fig. 7). The cod end is lined with stramin or with No. 14XXX silk grit gauze. Since the diving vane of the trawl exerted a strong depressing action, no extra weights were needed.

This trawl was hauled from the *Manning* and the *Smith* at speeds of 4 to 6 knots, on a towline of ¼-inch wire rope. At these speeds and with 100 to 300 meters of wire out, the towing tension ranged from 600 to 1,200 pounds.

Devereaux and Winsett (1953) provide data on the shape of the towing wire for the 10- and 15-foot models of the Isaacs-Kidd trawl during towing. Because of the depressing action of the diving vane, the straight-line assumption could not be applied when we calculated hauling depths. Since a suitable depth meter was not available, we estimated the curvature of the towing wire and the trawl depth by a method described by Hida and King (1955), which required frequent measurement during the haul of wire angle and amount

TABLE 3.—*Towing tensions obtained with the 1-meter ring trawl, measured with a dynamometer, on* Charles H. Gilbert *cruise 13*

Wire out	Main engine speed	Estimated vessel speed	Towing tension	
			Minimum	Maximum
	R.p.m.	*Knots*	*Pounds*	*Pounds*
195 meters	550	5.9	130	260
195 meters	700	6.7	200	390
195 meters	800	7.2	280	620
195 meters	900	7.7	390	720
195 meters	950	7.9	440	750
195 meters	1,000	8.1	440	1,005
575 meters	1,000	8.1	620	880
990 meters	1,000	8.1	...	1,080
975 meters	1,000	8.1	...	1,500

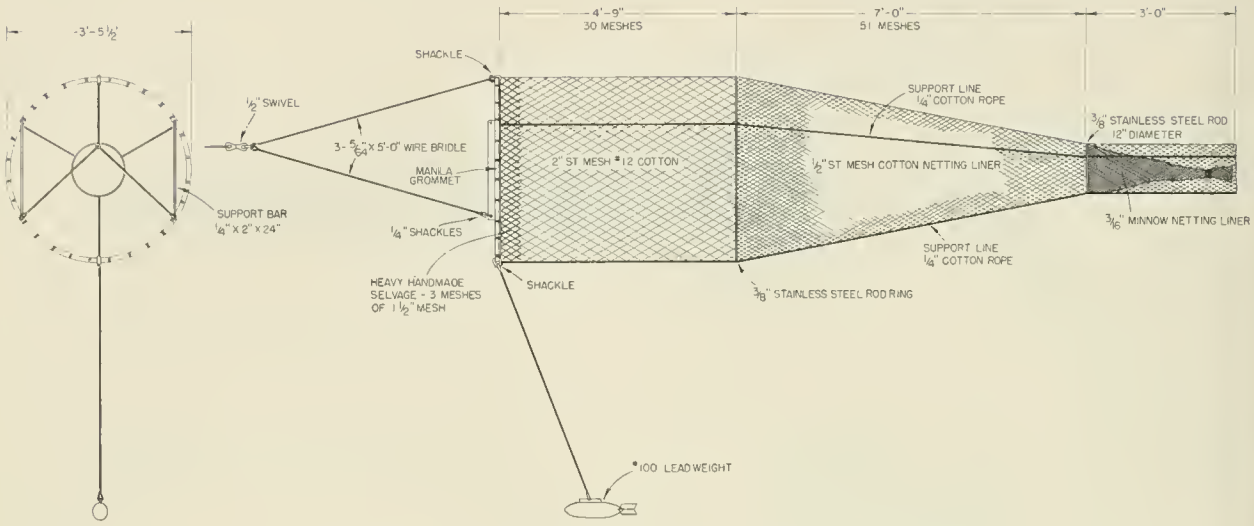

FIGURE 6.—Diagram of the 1-meter ring trawl, showing arrangement of bridle lines and streamlined lead weight.

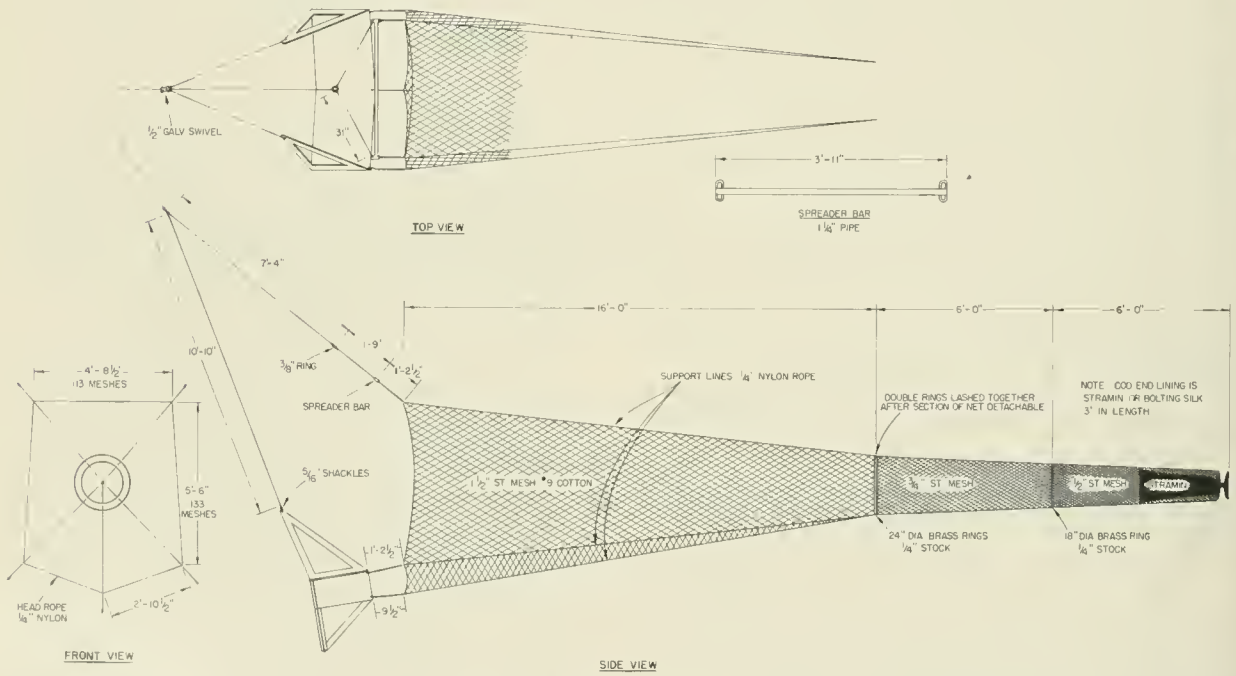

FIGURE 7.—Diagram of the 6-foot Isaacs-Kidd trawl used in central Pacific studies by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

of wire out. Depth conversion factors (table 4) were calculated from plots of these data.

TABLE 4.—*Depth conversion factors used to estimate depth of haul for 6-foot Isaacs-Kidd trawl*

[Wire out (in meters) × factor = trawl depth (in meters)]

Wire angle	Depth conversion factor	Cosine [1]
68°	0.44	0.375
69°	.42	.358
70°	.40	.342
71°	.38	.326
72°	.36	.309
73°	.34	.292
74°	.32	.276
75°	.31	.259
76°	.30	.242

[1] Cosine of the wire angle, the appropriate conversion factor if the towing wire described a straight line, is given for comparison.

10-FOOT ISAACS-KIDD TRAWL

Since the 10-foot trawl used in this study by the Laboratory in Honolulu has been considerably modified from the original plans given by Devereaux and Winsett (1953), we shall provide a detailed description of the main features of the gear.

Trawl Net

A schematic view of the net is shown in figure 8 and detailed plans are given in figure 9.

The front section of the net, about 27 feet in length, is made of 1½-inch mesh (stretched measure), double-knotted, No. 207 nylon twine, dyed red. The mesh counts for tapering the top, bottom, and side panels are shown in detail "A" (fig. 9). The headlines and other supporting lines are of ⅜-inch 3-strand nylon. The headline is attached to the diving vane by wire pennants of ¼-inch-diameter 7 x 19 stainless steel wire Nico-

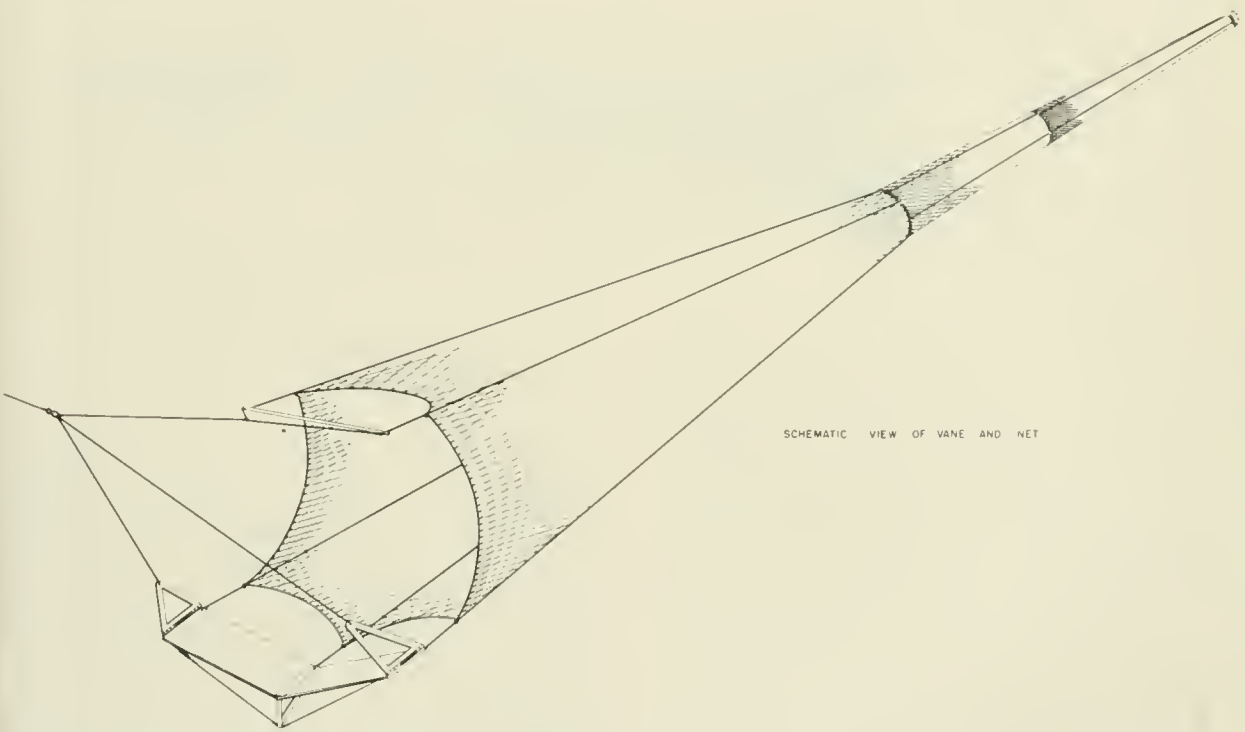

FIGURE 8.—Schematic view of the 10-foot Isaacs-Kidd trawl used by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

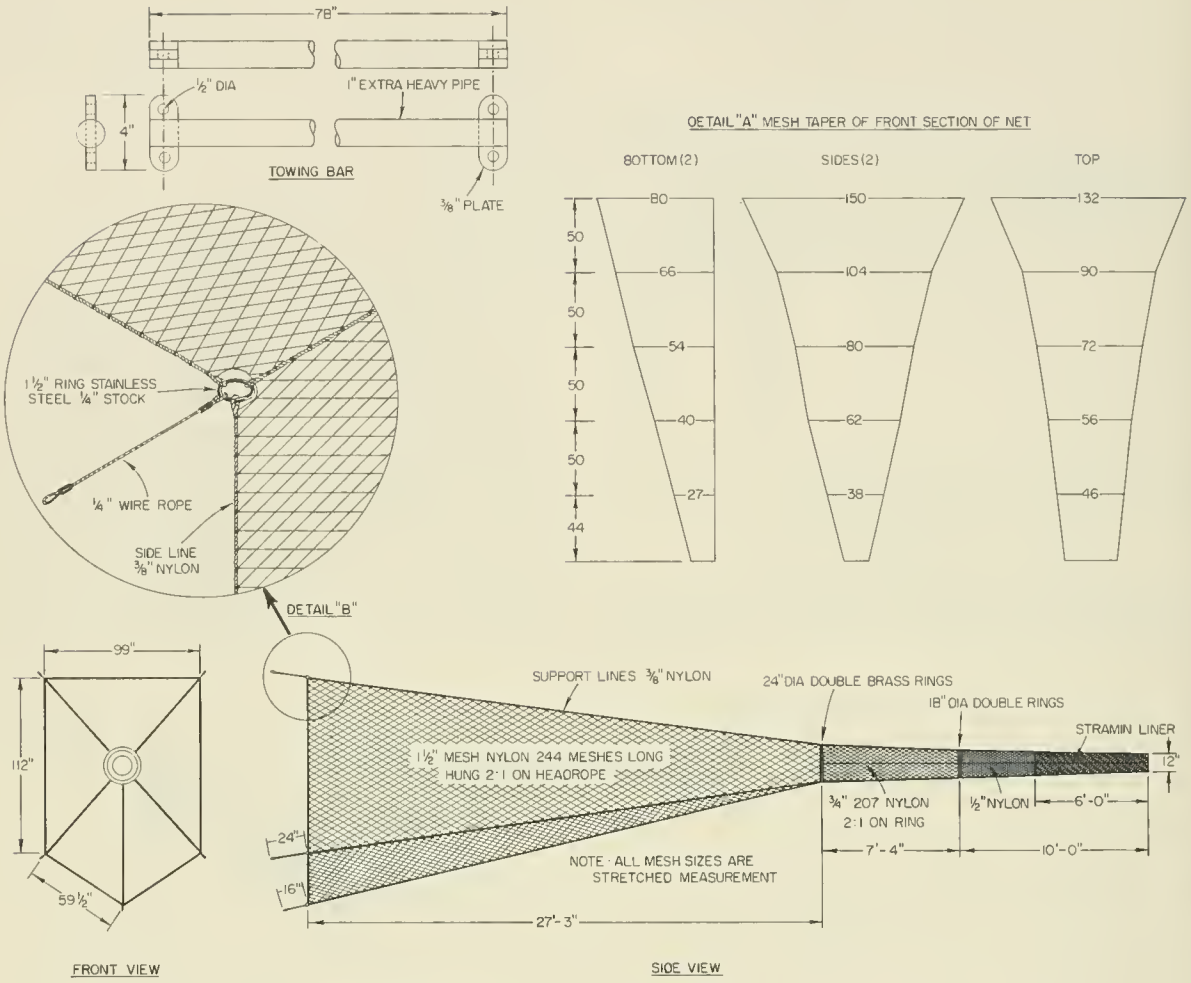

FIGURE 9.—Construction details of the 10-foot Isaacs-Kidd trawl net.

pressed to stainless rings (shown in detail "B," fig. 9).

The midregion of the net, 7 feet 4 inches in length, consists of a circular tapered section of ¾-inch mesh No. 207 nylon, detachable from both front section and cod end by a system of double rings lashed together with No. 207 nylon twine. Rings are of ¼-inch brass rod, 24 inches in diameter at the front of the section, 18 inches in diameter at the after end. Four equally spaced support lines of 3-strand 5/16-inch nylon are eye-spliced into a ring at each end of the section.

The cod end is a circular tapering section, 10 feet in length, of ½-inch mesh No. 207 nylon. The last 6 feet of this section is lined with stramin, coarse silk grit gauze, or fine-meshed nylon netting, which is attached at its forward margin to the main net.

Diving Vane

Plans of the diving vane are shown in figure 10. The body of the vane is formed of ⅛-inch steel plate, 24 inches in width and 10 feet 10 inches in length, bent at the midpoint to form an angle of 140°. The leading edge (section A–A, fig. 10) is reinforced by a 1 x 2-inch channel iron welded to the underside of the plate. A streamlined entry is formed by pressing a 1½-inch angle iron to shape and welding it to the plate and channel as shown. The leading edge is faired at the after-side by a strip of ⅛-inch plate 2 inches wide welded to both the channel iron and the plate. All of these welds are continuous and the entire leading edge assembly is made watertight to avoid corrosion from the inside. Holes ¾-inch in diameter

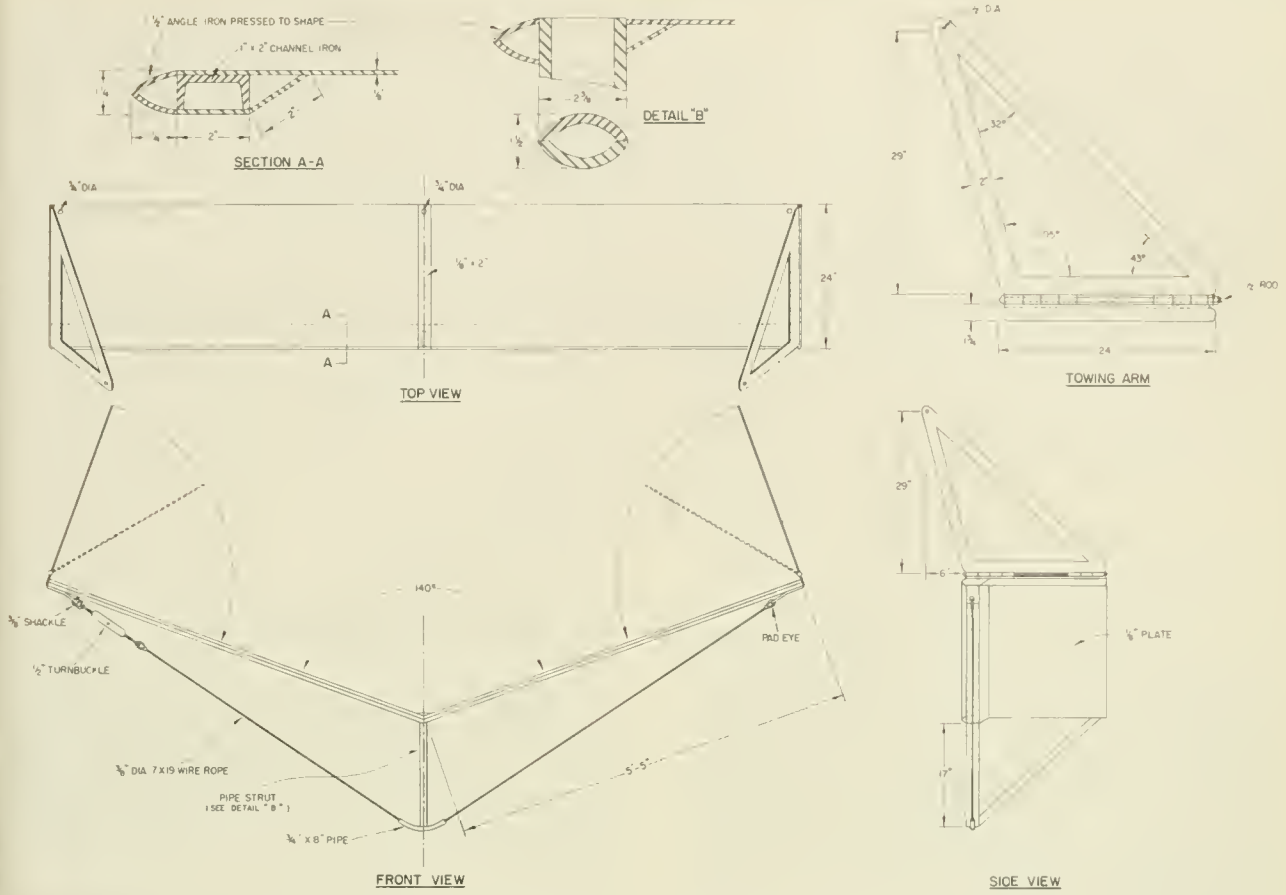

FIGURE 10.—Construction details of the diving vane of the 10-foot Isaacs-Kidd trawl.

are drilled on the midline and ends of the vane with their centers 1 inch from the after edge of the vane.

A pipe strut 17 inches in length extends downward from the front center of the vane (detail B, fig. 10). Lengths of 6-inch pipe are split lengthwise and welded together to form a faired cross section. This strut extends up through the leading edge of the vane and is welded both above and below. A 2-inch-wide center strip of ⅛-inch plate covers this point and adds stiffening to the vane.

The tension member consists of a wire pennant made from ⅜-inch-diameter 7×19 preformed stainless steel wire rope. Solid rigging thimbles are installed at each end. The tension adjustment is made with a ⅝-inch closed pipe turnbuckle secured by ⅜-inch galvanized chain shackles. Pad eyes of ⅜-inch plate drilled for ⅜-inch shackles are welded to the vane at each end. An 8-inch length of ¾-inch pipe is bent around a suitable radius and welded to the lower end of the pipe strut to serve as a guide for the tension member. Tension on the wire should not be excessive; the wire after prestretching should be just hand-tight since too much tension during towing will cause the vane to buckle.

The towing arms are hinged triangular members formed by welding ¼ x 2-inch plate bars into a triangle with the towing center 6 inches forward of the leading edge and 29½ inches above the hinge center. The arms are hinged by means of a ½-inch diameter galvanized pin held by 2-inch-long

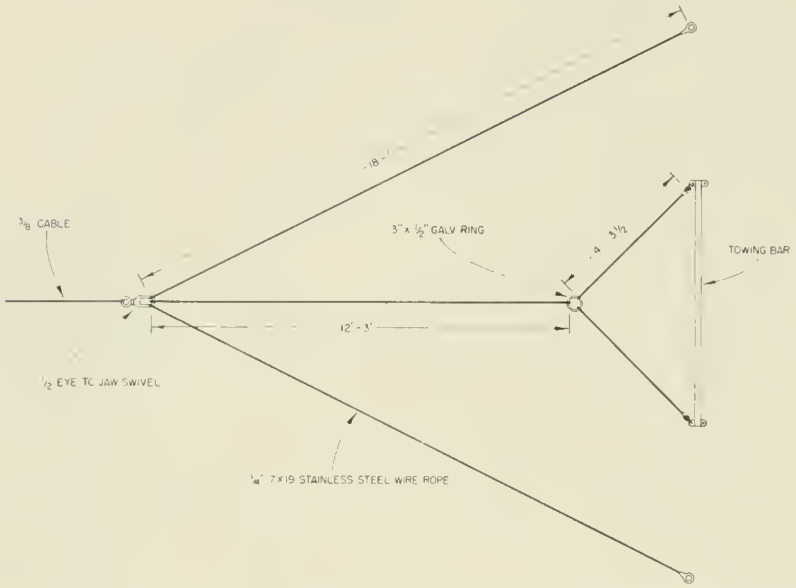

FIGURE 11.—Towing bridle and spreader bar used with the 10-foot Isaacs-Kidd trawl.

sections of ¾-inch pipe welded alternately to the towing arm and to the end plate of the vane. This plate is fabricated from ¼-inch plate 1¾ inches wide. All leading edges of the towing arms are ground to a thin edge and the hinge pin head is turned to a point to minimize resistance and turbulence during towing.

After final assembly the vane is thoroughly sandblasted and galvanized.

Towing Bridle and Spreader Bar

Details of the rigging of the towing bridle are shown in figure 11. All sections are made of ¼-inch-diameter 7×19 preformed stainless steel wire rope. The spreader bar is a 78-inch length of heavy pipe with 4-inch bars welded at each end and drilled to take ⅜-inch shackles.

Hauling Methods

The 10-foot Isaacs-Kidd trawl was hauled by the *Smith* at speeds of 4 to 6 knots, on a towing line of ⅜-inch wire rope. At 5 knots, with about 800 meters of wire out and a wire angle of 71°, the towing tension ranged from 1,750 to 2,600 pounds; at 6 knots, with the same amount of wire out and a wire angle of 73°, the towing tension was 2,000 to 3,000 pounds.

As previously mentioned, data on the shape of the towing wire during hauling of 10- and 15-foot Isaacs-Kidd trawls have been given by Devereaux and Winsett (1953). We have independently calculated the trawl depth by the method described by Hida and King (1955), based on measurements of wire angle and wire out. Depth conversion factors derived from these measurements are listed in table 5.

TABLE 5.—*Depth conversion factors used to estimate depth of haul for 10-foot Isaacs-Kidd trawl*

[Wire out (in meters) × factor = trawl depth (in meters)]

Wire angle	Depth conversion factor
66°	0.46
67°	0.45
68°	0.44
69°	0.43
70°	0.42
71°	0.41
72°	0.40
73°	0.39
74°	0.38
75°	0.37
76°	0.36

LABORATORY PROCEDURES

The trawl collection, drained of the preserving liquid, was spread out in a shallow, white-enameled pan and sorted into two size categories: organisms less than 2 cm. and organisms greater than 2 cm., greatest dimension. This separation was made since the first category was not judged to have been sampled in a quantitative manner because of the coarse mesh of the nets used. Each size group was further sorted into kinds of organisms, with

identifications being made to the most precise degree that seemed practical.

The number of individuals and displacement volume were determined for each kind or group of organisms identified. The minimum and maximum lengths, in millimeters, were recorded for each category of organisms. In some instances the total number of the more numerous organisms in the less-than-2-cm. category was estimated from the number in a subsample.

In examining the resulting data it was evident that those organisms less than 2 cm. in longest dimension usually constituted a very small fraction of the total volume of the catch. Of greater importance was the infrequent occurrence of organisms of large bulk. It was decided, therefore, to give in the summary tables (appendix tables 1 to 4) the number of organisms and the volume of the total catch, expressed in terms of 1 hour of hauling, with the two size categories combined but with added reference to the occasional occurrence of large numbers of small organisms, such as euphausiids, and the infrequent bulky forms, such as jellyfish or large fish, that greatly influenced the volume of the catch or the total number of individuals in it.

The nature of the trawling gear and the methods used did not permit or justify an exact quantitative evaluation of the catch. The amount of water strained on each haul was not metered. Vessel speed during hauling, however, was fairly uniform for each trawl, since an attempt was made to hold the wire angle within a narrow range of values. Although most hauls were for a period of 1 hour, the time varied somewhat, as indicated in appendix tables 1 to 4, and this variation was taken into account. Other possible sources of variation in the data were those relating to the hour of hauling and to depth of haul. The majority of the hauls, however, were made at night within 1 to 3 hours after sunset and sampled the upper ocean layer between the surface and 400 meters.

Detailed lists showing composition of the catches for each of the four trawls are given in appendix tables 5 to 8. Because of the great variety of invertebrates and fishes in the collections, it was not possible to give equal attention or bring the same skill to the identification of all groups. Major effort was spent on the euphausiids, shrimps, and stomiatoid and myctophid fishes because of their prominence in the collections. References used in the identification of the different groups are listed in the appendix (p. 304). Berg's (1947) system of classification and nomenclature was used in most respects for the family names of the fishes.

Where appropriate, the data were subjected to statistical analysis and the results expressed in terms of the probability that the event occurred by chance alone. We regarded events with $P \leqq 0.05$ as not occurring by chance and therefore of significance.

CATCHING ABILITIES OF THE FOUR TRAWLS

The catching ability, or efficiency, of a midwater trawl is related to many factors, including size of the mouth opening, mesh size of the net, and hauling speed, and also to the amount of disturbance or turbulence directly ahead of the net caused by the towing cable and bridle lines. These general features, except turbulence, are summarized in table 6 for the four trawls. The 1-meter ring trawl, which had the largest mesh and was towed at a slightly higher speed than the other three trawls, produced the poorest catches, both in number and in volume of organisms. As shown in figure 6, this trawl also had the most obstruction immediately ahead of the net; the other three trawls were much better designed in this respect.

TABLE 6.—*Factors affecting catching ability of the four trawls used*

Factor	6-foot beam	1-meter ring	Isaacs-Kidd	
			6-foot	10-foot
Size of mouth opening (sq. ft.)	36.0	8.4	29.8	88.3.
Mesh size:				
Front and midsection (stretched measure)	1-inch	2-inches	1½- and ¾-inch	1½- and ¾-inch.
Cod end liner (straight measure)	3/16-inch	½- and 3/16-inch	⅜-inch (stramin or equivalent)	⅜-inch (stramin or equivalent).
Hauling speed	4–5 knots	6–7 knots	4–6 knots	4–6 knots.

Although the amount of water strained by our midwater trawls was not metered, it can be estimated fairly accurately if we can accept certain assumptions; namely, that (1) the hauls were made at uniform speed; (2) the nets were 100 percent efficient, i.e., all of the water entering the mouth of the net passed on through; and (3) the amount of water strained was, therefore, proportional to the area of the mouth opening. It must be admitted that these assumptions may include some error, but we believe that for our purposes here they can reasonably be applied to the Isaacs-Kidd trawls. The nets had a high ratio of length to mouth opening and were of relatively coarse mesh, except for the cod end. There was never any evidence of clogging. Vessel speed was adjusted during the tows to yield a wire angle of 70°–72°, and the actual hauling speed was generally maintained within a range of 4 to 6 knots. If we accept 5 knots as the average hauling speed, in 1 hour the 6-foot trawl would strain 25,663 cubic meters of water and the 10-foot trawl would strain 76,043 cubic meters.

We have calculated average values in terms of number and volume of organisms in the total catch, for each of the four trawls for each major geographic region investigated (table 7). The results show considerable variation, part of which is influenced by the large numbers of euphausiids and barnacle larvae obtained in the North Pacific with the two Isaacs-Kidd trawls and by a few large catches, also of euphausiids, made in the equatorial Pacific with the 6-foot beam trawl. The volume of catch varies generally with the size of the trawl. When evaluated in terms of volume of catch per unit of mouth area, we find that the two Isaacs-Kidd trawls were on the average about equal in catching efficiency; they showed no marked superiority over the 6-foot beam trawl or the 1-meter ring trawl when used in Hawaiian waters, and were even slightly inferior to the 6-foot beam trawl when operating in the equatorial Pacific.

The average individual size (ml.) of organisms in the catch varied inversely with the relative amount of fine-meshed netting used to line the cod ends of the trawl nets. The net with the largest mouth diameter caught, on the average, the largest organisms. The net with the smallest mouth diameter did not catch the smallest organisms, however, because its cod-end liner was of slightly larger mesh than that used in the other three trawls.

TABLE 7.—*Number of organisms and volume of catches made with the four trawls, in relation to size of mouth opening of the trawl net and to geographic region*

[Number of quantitative hauls in parentheses]

Region	6-foot beam	1-meter ring	Isaacs-Kidd	
			6-foot	10-foot
Average number of organisms per hour of hauling:				
North Pacific			5,615 (26)	1,485 (32)
Hawaiian waters	130 (10)	68 (23)	322 (19)	314 (24)
Equatorial Pacific	3,234 (6)		600 (33)	657 (101)
Average	1,294 (16)	68 (23)	2,204 (78)	773 (157)
Average volume (ml.) of catch per hour of hauling:				
North Pacific			59.3	165.3
Hawaiian waters	22.4	5.4	22.4	88.2
Equatorial Pacific	147.6		103.2	232.9
Average	69.3	5.4	68.9	197.0
Average number of organisms per hour per square foot of mouth opening:				
North Pacific			188.4	16.8
Hawaiian waters	3.6	8.0	10.8	3.6
Equatorial Pacific	89.8		20.1	7.4
Average	35.9	8.0	74.0	8.8
Average volume (ml.) of catch per hour per square foot of mouth opening:				
North Pacific			2.0	1.9
Hawaiian waters	.6	.6	.8	1.0
Equatorial Pacific	4.1		3.5	2.6
Average	1.9	.6	2.3	2.2
Average individual size (ml.) of organisms in the catch:[1]				
All areas	.05	.08	.03	.25

[1] Average volume of catch divided by average number of organisms.

On *Smith* cruise 27 to the central North Pacific, the 6- and 10-foot Isaacs-Kidd trawls were used on consecutive hauls on three successive nights for the purpose of comparing the catches obtained with the two sizes of gear. The results of the test, summarized in table 8, indicate that the catch of the larger trawl was about three times as great, with respect both to volume and to number of organisms, as that of the smaller trawl. When judged in terms of catch per unit of mouth area, the two trawls took essentially the same volume and number of organisms. The kinds and sizes of organisms in the collections were also similar for the two trawls.

A checklist of organisms identified in the catch of the four trawls is given in appendix tables 5 to 8. In general, the greater the number of hauls and the more regions sampled by a trawl, the longer the list. A study of appendix tables 5 to

TABLE 8.—*Volume and number of organisms obtained with the Isaacs-Kidd trawls on* Hugh M. Smith *cruise 27, central North Pacific, 1955*

Item	6-foot	10-foot
Station 23:		
Position:		
Latitude	28°28′ N.	28°32′ N.
Longitude	178°10′ W.	178°10′ W.
Date	Jan. 31	Jan. 31
Time of haul (zone time)	1948–2049	2102–2202
Estimated maximum depth (m.)	122	118
Catch per hour's hauling:		
Volume (ml.)	6.7	57.1
Number of organisms	265	882
Station 25:		
Position:		
Latitude	30°02′ N.	29°56′ N.
Longitude	179°31′ E.	179°28′ E.
Date	Feb. 1	Feb. 1
Time of haul (zone time)	2049–2151	1939–2041
Estimated maximum depth (m.)	122	118
Catch per hour's hauling:		
Volume (ml.)	28.1	62.1
Number of organisms	1,487	3,629
Station 28:		
Position:		
Latitude	32°52′ N.	32°46′ N.
Longitude	179°55′ W.	179°54′ W.
Date	Feb. 2	Feb. 2
Time of haul (zone time)	2049–2149	1943–2042
Estimated maximum depth (m.)	144	118
Catch per hour's hauling:		
Volume (ml.)	56.1	177.7
Number of organisms	542	1,456
Average (all stations):		
Per hour of hauling:		
Volume (ml.)	30.3	99.0
Number of organisms	765	1,989
Per 1,000 $m.^3$ of water strained:		
Volume (ml.)	1.2	1.3
Number of organisms	29.8	26.2

8 shows that many groups of vertebrates and invertebrates were common to the catch of all four trawls. In an attempt to determine whether there were wide differences in the catch composition, we counted the major categories appearing in each list and assembled the results in table 9. The same number of phyla and classes was sampled by all four trawls. The major differences were in the families of invertebrates and the families and genera of fishes, with the most-frequently used trawl catching the greatest variety of organisms.

VARIATION OF TRAWL CATCH

DIURNAL VARIATION

Size of Catch

Although our data indicate that catches made at night greatly exceeded day catches both in volume and number of organisms (table 10), the information available is insufficient to describe the diurnal variation in forage abundance. On *Manning* cruise 9 (appendix table 1) two series of four hauls each were made with the 6-foot beam trawl with the stations at various distances from shore, one series in the daytime (1000–1800 hours) and the other at night (2000–0300 hours). The day hauls yielded an average volume of 8.6 ml. per hour of hauling and the night hauls 38.6 ml.; the night/day volume ratio was therefore 4.49. With respect to number, day hauls produced an average of 123 organisms and the night hauls 134, for a night/day ratio of 1.09. The difference between these two ratios indicates a difference in the size of organisms in the night and day catches. When the average volume is divided by the average number in the catch we obtain a value of 0.07 ml. for the average individual size of the organisms in the day catches and 0.29 ml. for the individual size in the night catches.

In April–June 1953, the 1-meter ring trawl was used repeatedly at two "fixed" stations in Hawaiian waters, one located to windward and the other to leeward of the islands. The stations were about 75 miles apart, and both were thought to represent open ocean conditions. On each of the *Gilbert* cruises 11, 12, and 13, the windward station (station A) was visited during the early afternoon hours and the leeward station (station D)

TABLE 9.—*Number of taxonomic groups in the catch of the four trawls and in the stomach contents of tuna*

	Invertebrates				Vertebrates (Pisces)		Number of hauls or stomachs	Authority
	Phyla or subphyla	Classes	Orders	Families	Families	Genera		
Gear:								
6-foot beam trawl	6	8	12	19	17	26	16	
1-meter ring trawl	6	6	12	15	12	11	23	
Isaacs-Kidd trawl:								
6-foot	7	7	15	25	33	42	78	
10-foot	7	7	16	30	53	77	157	
Stomach contents:								
Yellowfin	3	5	11	19	37	19	1,097	Reintjes and King (1953).
Do	3	4	12	31	48	52	439	King and Ikehara (1956).
Bigeye	4	4	9	22	36	38	166	Do.
Skipjack	3	5	11	17	42	30	707	Waldron and King.[1]
Albacore	5	6	12	29	34	24	348	Iversen (in press).

[1] See footnote 4, p. 295.

TABLE 10.—*Quantitative differences in the catch of day and night hauls with three types of trawls*

[Based on 40 hauls]

Trawl and vessel	Cruise	Area	Day hauls			Night hauls			Night/day ratio		Average size of organism [1]	
			Number of hauls	Average volume	Average number of organisms	Number of hauls	Average volume	Average number of organisms	Volume of catch	Number of organisms	Day	Night
				Milliliters			*Milliliters*		*Milliliters*		*Milliliters*	*Milliliters*
6-foot beam trawl:												
John R. Manning	9	Hawaiian waters	4	8.6	123	4	38.6	134	4.49	1.09	0.07	0.29
1-meter ring trawl:												
Charles H. Gilbert	11, 12, 13	Hawaiian waters	11	1.8	47	11	9.0	93	4.90	1.98	.04	.10
6-foot Isaacs-Kidd trawl:												
John R. Manning	20	Hawaiian waters	2	5.8	106	2	22.8	257	3.91	2.42	.06	.09
Do	20	Equatorial Pacific [2]	4	11.4	158	2	106.4	614	9.33	3.89	.07	.17

[1] Displacement volume.
[2] Countercurrent.

shortly after midnight. Although minor differences between these two stations in the physical and chemical features of the environment might have influenced the abundance of forage organisms, we believe that the major differences in the catch were related to the time of hauling. The average volume of 11 hauls at station A was 1.8 ml. and the average number of organisms in the catch was 47, as compared with an average volume of 9.0 ml. and an average number of 93 for 11 hauls at station D. The night/day ratio for volumes was 4.90, and for numbers, 1.98. The average individual size of organisms was 0.04 ml. for the day hauls and 0.10 ml. for the night hauls.

At the start of *Manning* cruise 20, four test hauls were made with the 6-foot Isaacs-Kidd trawl in Hawaiian waters to determine the difference in catch between hauls made in the morning about 2 hours after sunrise and at night about 1 hour after sunset. For this series the average volume of the two night samples was 22.8 ml. and the average number of organisms was 257; for the two day samples, the average volume was 5.8 ml. and the average number of organisms was 106. The night/day ratio was 3.91 for volume and 2.42 for number of organisms. Again the average size of organisms was much larger in night than in day hauls (table 10).

The main objective of *Manning* cruise 20 was to conduct longline fishing in the equatorial Pacific. During the first 4 days of operations in the Countercurrent, a trawl haul was made each morning about 2 hours after sunrise, soon after the longline had been set. Because of the poor catches that were being made, the hauling time was changed on the 5th day to about 1 hour after sunset, just after the longline gear had been retrieved for the day and the ship was underway to the next station. The two hauls made at this new time were also in the Countercurrent, and averaged 106.4 ml. in volume, as compared with an average of 11.4 ml. for the four day hauls taken earlier. The average numbers of organisms, night/day ratios, and average size of the organisms are given in table 10, along with similar data for the other cruises mentioned. No day hauls were made with the 10-foot Isaacs-Kidd trawl.

Composition of the Catch

There were also marked diurnal differences in the composition of the trawl catches. Lists of organisms occurring in the day and night hauls referred to above are given in tables 11 and 12 and appendix table 6 and summarized by general category in table 13. Coelenterates, certain molluscs, and tunicates occurred in about equal frequency in the day and night collections. Among the Crustacea, the amphipods and stomatopods were taken in about equal numbers in day and night hauls, whereas the decapods were taken principally at night. Very few squids and fishes, except larval and juvenile forms, were captured during daylight. The main difference, therefore, between day and night hauls was the capture at night of the stronger swimming animals which were either absent from the upper layer during the day or were able to dodge the net. We suspect that most of these animals were capable of making extensive vertical migrations during the day to depths below those sampled by the trawls and became concen-

TABLE 11.—*Composition of catches obtained in four day hauls and four night hauls with the 6-foot beam trawl in Hawaiian waters*, John R. Manning *cruise 9, November 1951*

Organisms	Day		Night	
	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
COELENTERATA: Unidentified	50	1	75	(1)
Hydrozoa:				
Siphonophora	50	(1)	25	35
Medusae: Unidentified			50	2
CHAETOGNATHA: Unidentified	100	50	100	14
Sagitta sp.	50	24		
ARTHROPODA:				
Crustacea:				
Copepoda			25	(1)
Mysidacea:				
Lophogastridae			25	10
Amphipoda:				
Oxycephalidae:				
Rhabdosoma sp.			25	1
Stomatopoda (larvae)	75	55	100	27
Euphausiacea	50	15	75	29
Decapoda:				
Penaeidae:				
Gennadas sp.			50	3
Pandalidae:				
Parapandalus zur strasseni	25	3	25	2
Hoplophoridae:				
Hoplophorus gracilirostris			50	2
H. grimaldii	25	1		
Systelaspis debilis			25	2
Sergestidae: Unidentified	25	10	50	6
Sergestes gardineri			50	5
Sergestes sp.			25	22
Scyllaridae: Phyllosoma	25	1		
Unidentified Decapoda	25	(1)	50	(1)
Unidentified Crustacea	75	(1)	25	(1)
MOLLUSCA:				
Gastropoda:				
Pteropoda	25	(1)		
Heteropoda:				
Pterotracheidae	75	3	25	6
Cephalopoda:				
Decapoda (squids)	25	7		
Chiroteuthidae			25	1
Unidentified Mollusca	25	(1)		
UNIDENTIFIABLE INVERTEBRATE MATERIAL	75	(1)	75	(1)
CHORDATA—Tunicata:				
Thaliacea:				
Pyrosomatidae	25	18		
Salpidae	25	35		
Unidentified Tunicata	50	(1)	50	(1)
CHORDATA—Vertebrata:				
Pisces:				
Gonostomidae:				
Vinciguerria lucetia			25	1
Chauliodontidae:				
Chauliodus sp.			25	1
Astronesthidae:				
Astronesthes lucifer			25	1
Idiacanthidae	25	1		
Synodontidae			25	1
Myctophidae: Unidentified	25	13	75	7
Benthosema sp.	25	1	25	4
Diogenichthys atlanticus	25	1		
Centrobranchus nigro-ocellatus			25	1
Myctophum brachynathos			25	2
M. spinosum			25	1
M. evermanni			25	4
Notolychnus valdiviae			50	4
Diaphus sp.	25	2	75	3
Lampanyctus pyrsobolus			25	1
Lampanyctus sp.	25	1	50	18
Ceratoscopelus townsendi			50	4
Apogonidae			25	1
Acanthuridae			25	1
Larval fish:				
Leptocephali: Unidentified	50	1	50	1
Unidentified larvae	100	10	100	32
Unidentified Pisces			25	1

[1] Actual number not determined.

TABLE 12.—*Composition of catches obtained in six day hauls and four night hauls with 6-foot Isaacs-Kidd trawl in Hawaiian waters and in the Equatorial Countercurrent*, John R. Manning *cruise 20, April–May 1954*

Organisms	Day		Night	
	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
COELENTERATA:				
Hydrozoa:				
Siphonophora	100	27	100	32
Medusae: Unidentified	17	1	25	1
CTENOPHORA: Unidentified			75	5
CHAETOGNATHA: Unidentified	100	78	100	66
ARTHROPODA:				
Crustacea:				
Mysidacea:				
Lophogastridae			25	1
Amphipoda:				
Phronimidae:				
Phronima sp.	33	1	50	2
Oxycephalidae:				
Oxycephalus sp.			25	2
Rhabdosoma sp.	67	1	50	5
Unidentified Amphipoda	67	71	50	32
Stomatopoda (larvae)	33	2		
Euphausiacea			50	370
Decapoda:				
Penaeidae:				
Gennadas scutatus			25	20
Gennadas sp.			25	8
Funchalia taaningi			25	1
Pandalidae:				
Parapandalus zur strasseni			50	6
Heterocarpus ensifer			25	1
Hoplophoridae:				
Hoplophorus typus			25	1
H. gracilirostris			25	1
Sergestidae:				
Sergestes gardineri			25	1
Sergestes sp.			50	6
Palinuridae: Phyllosoma	17	1		
Unidentified Decapoda	33	22		
Unidentified Crustacea			100	34
MOLLUSCA:				
Gastropoda:				
Heteropoda:				
Pterotracheidae			75	2
Cephalopoda:				
Decapoda (squids):				
Cranchiidae	17	2	25	1
Unidentified Mollusca	17	2	50	10
UNIDENTIFIABLE INVERTEBRATE MATERIAL	33	(1)	25	(1)
CHORDATA—Tunicata:				
Thaliacea:				
Pyrosomatidae	17	1	50	21
Salpidae	83	7	50	12
Unidentified Tunicata	67	11	100	20
CHORDATA—Vertebrata:				
Pisces:				
Gonostomidae: Unidentified			25	1
Vinciguerria lucetia			25	6
Gonostoma elongatum			50	2
Diplophos taenia			25	4
Stomiatidae: Unidentified			25	2
Thysanactis denter			25	1
Thysanactis sp.			25	2
Eustomias sp.			50	4
Malacosteidae:				
Photostomias sp.			50	2
Aristostomias sp.			25	2
Paralepididae: Unidentified			25	7
Myctophidae:				
Myctophum evermanni			25	2
M. affine			25	1
Diaphus sp.			50	2
Lampanyctus pyrsobolus			25	2
Lampanyctus sp.			50	4
Ceratoscopelus townsendi			25	1
Bregmacerotidae:				
Bregmaceros macclellandi			25	4
Gempylidae: Unidentified	17	1		
Tetragonuridae:				
Tetragonurus sp.			25	1
Larval fish:				
Leptocephali: Unidentified	33	2	50	1
Unidentified larvae	100	5	100	21
Unidentified Pisces			50	2

[1] Actual number not determined.

TABLE 13.—*Number of categories of organisms taken in comparable day and night hauls, by trawl*

[Based on tables 11 and 12 and appendix table 6]

Gear and cruise	Area	Number of hauls		Coelenterata		Decapod Crustacea		Other Crustacea		Mollusca		Tunicata		Pisces	
		Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
6-foot beam trawl:															
John R. Manning:															
Cruise 9	Hawaiian waters	4	4	2	3	5	8	3	6	4	2	3	-------	8	20
1-meter ring trawl:															
Charles H. Gilbert:															
Cruise 11	Hawaiian waters	11	12	2	2	3	9	8	8	7	6	3	3	7	17
Cruise 12	----do														
Cruise 13	----do														
Hugh M. Smith:															
Cruise 21	----do														
6-foot Isaacs-Kidd trawl:															
John R. Manning:															
Cruise 20	Hawaiian waters	2	2	2	2	2	9	4	7	2	3	3	3	3	22
	Equatorial Countercurrent	4	2												

trated in the upper layer of the ocean only at night, so that the augmentation of the fauna in the upper strata at night was most likely the more important cause of the day/night difference in our catch.

Aron (1959) presents interesting data on diurnal variation in midwater trawl catches obtained with a modified Isaacs-Kidd trawl in the northeastern Pacific. He also found wide differences between day and night hauls, but through the use of stratified tows was able to show that day/night differences in the catch diminished with increasing depth between the surface and 250 meters. For night hauls he reports a general decrease in the catch with an increase in depth and just the reverse for day hauls.

VARIATION WITH AREA AND CURRENT SYSTEM

The general pattern of ocean currents in the Pacific has been described by Schott (1935, p. 161–171, plates XXIX and XXX) and by Sverdrup et al. (1942, p. 698–728, chart VII). Figure 12 is a diagrammatic representation of the gross features of the current system of the central Pacific region in relation to the boundaries of seven "faunal zones" selected by us for use in comparing latitudinal differences in the trawl catch. As far as possible the boundaries of the different zones were chosen to coincide with natural subdivisions of the environment. Zone 1 extends from the limits of our sampling in the south (about latitude 19° S.) to latitude 5° S. in the north, within the South Equatorial Current (SEC); zone 2 brackets the region of upwelling and enrichment at the Equator and extends from 5° S. to the northern boundary of the South Equatorial Current (SEC) at about 5° N.; zone 3 is the Equatorial Countercurrent (ECC) between approximately latitude 5° N. and 10° N.; zone 4, the North Equatorial Current (NEC) between the northern boundary of the Equatorial Countercurrent and waters adjacent to the Hawaiian Islands; zone 5, the Hawaiian Islands (H) from about latitude 18° N. to 28° N.; zone 6, the North Pacific Current (NPC) between Hawaiian waters and 35° N., the approximate center of the "transition zone" of McGary et al. (1958), which is the zone of convergence between the Central Water Mass on the south and the Subarctic Water Mass on the north; and zone 7, the Aleutian Current (AC) from 35° N. to about 50° N., the northern limit of our sampling. The representation of the South Equatorial Current (zone 1) does not take into con-

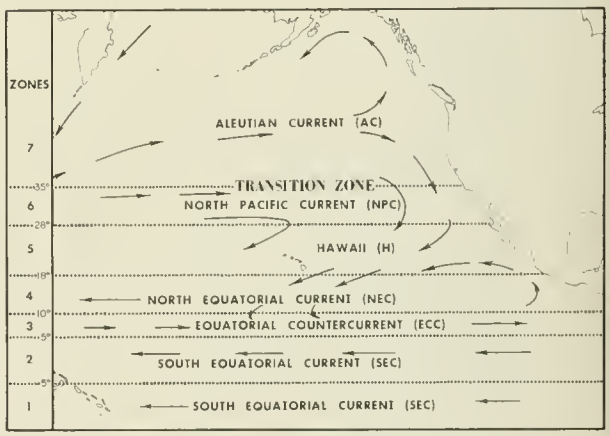

FIGURE 12.—Bounndaries of the seven "faunal zones" employed in the comparison of latitudinal variations in the trawl catch, in relation to the major features of the ocean current system in the central Pacific.

sideration Reid's (1959) report of a weak easterly countercurrent near 10° S.

Variation in Size of Catch

Latitudinal variations.—Since the major environmental boundaries or discontinuities in the central Pacific are zonal, i.e., east-west in alinement, we assumed that variations in trawl catch associated with longitude would be of much less significance than the latitudinal variations. Therefore, in order to examine major variations in the data with respect to the current system, the catch data for the 6- and 10-foot Isaacs-Kidd trawls were combined over the longitudes sampled but segregated according to the latitudinal zones we have defined.

The results, shown in figure 13, demonstrate a marked variation with latitude in the abundance of forage organisms sampled with the Isaacs-Kidd trawls. With respect to volume,[2] the curves were similar for both trawls, with peak values recorded for each trawl in the same zones. With respect to number of organisms, the catch was similar for the two trawls except in the most northern zones, where the data were strongly influenced by a few large catches of euphausiids and barnacle larvae. These organisms were particularly abundant in catches of the 6-foot trawl on *Manning* cruise 22 in September 1954 and account for the major difference between the two trawls in the Aleutian Current and in the North Pacific Current. Both trawls, however, captured the largest numbers of organisms in the northern zones, with a secondary peak at the Equator.

The least productive areas, with respect to both volume and number of organisms, were the South Equatorial Current south of latitude 5° S., the North Equatorial Current between about latitudes 10° N. and 18° N., and waters around the Hawaiian Islands.

One interesting feature of the data, illustrated in figure 13, is the increase of variance, particularly in numbers of organisms, in the northern zones. This increase is indicated by the width of the 0.95 fiducial interval shown for each mean. McGary et al. (1958) have pointed out that this northern region is an area of great complexity and

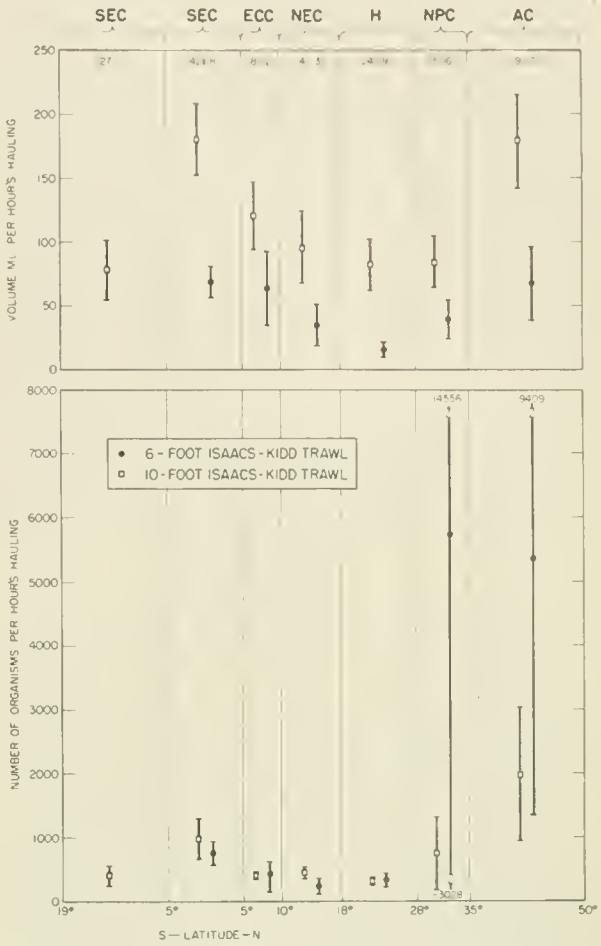

FIGURE 13.—Variation with latitude in average volumes and numbers of organisms captured per hour of hauling with the 6- and 10-foot Isaacs-Kidd trawls. (The limits of the 0.95 fiducial interval are indicated for each mean; the number of samples for each area is shown in parentheses. Zones defined in figure 12.)

of wide fluctuations, both seasonally and otherwise, in such features as temperature, salinity, phosphate concentration, and zooplankton abundance. The high variance in the trawl catches may be related to these fluctuations in the environment in the northern waters, as contrasted with the comparatively stable conditions in tropical and subtropical waters.

Although the data obtained from the 1-meter ring trawl and the 6-foot beam trawl were not of sufficient geographic coverage to treat in a detailed manner, the catches of the beam trawl did show a marked difference between the two major areas sampled. For five night hauls of *Manning*

[2] The volumes used in this comparison were the total catches minus unusually large or bulky organisms constituting approximately 50 percent or more of the catch.

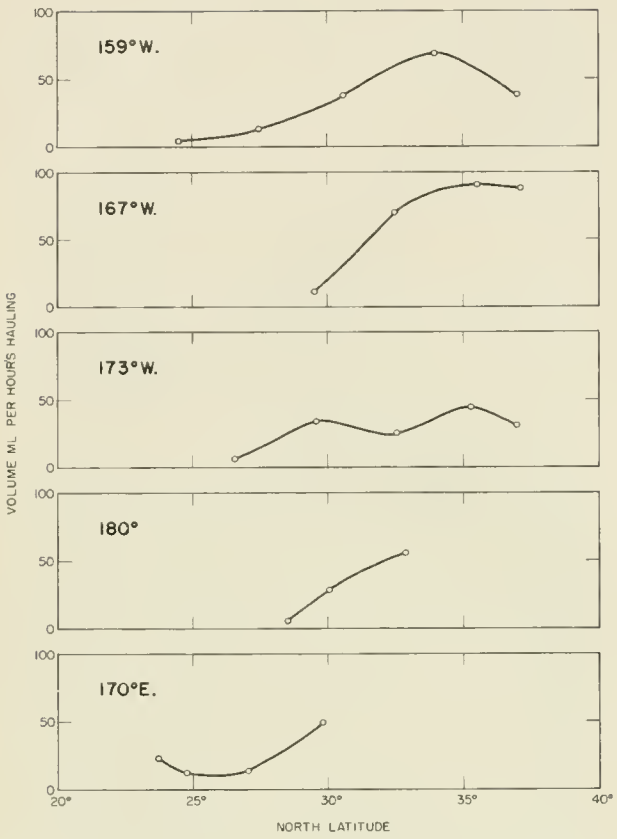

FIGURE 14.—Variation in trawl catch (volume in milliliters per hour of hauling) of 6-foot Isaacs-Kidd trawl on five north-south sections, *Hugh M. Smith* cruise 27, January–February 1955.

cruise 9 in November 1951 in Hawaiian waters, the average volume was 34.6 ml. and the average number of organisms was 138 per hour of hauling. Four night hauls of *Smith* cruise 15 in June 1952 at about latitude 6° N. in the Equatorial Countercurrent yielded an average volume of 217.9 ml. and an average number of 4,803 organisms. The chief difference in the composition of the catch from the two areas was the much greater quantity of euphausiids taken in the Countercurrent. The variety and quantity of fish captured in the two areas were approximately equal. Although the two cruises occurred at different times of the year, we do not believe that the differences observed were seasonal in nature, but rather were associated with geographical differences in the fauna or differences in standing crop of certain faunal groups.

Longitudinal variations.—The 6-foot Isaacs-Kidd trawl was employed on one cruise, *Smith* cruise 27, in such manner as to provide a rough evaluation of differences in the volume of catch among longitudes in the central North Pacific. During January and February 1955, three to five night hauls were made on north-south sections along the longitudes 170° E., 180°, 173° W., 167° W., and 159° W., within the latitudinal range of 23° N. to 37° N. As evidenced in figure 14, and evaluated by an analysis of variance, the differences among longitudes were not significant ($F=1.79$; d.f.=4 and 16; $P>0.05$); however, the residual variance in the test was composed of variability due to latitude as well as to chance, which reduced the F value for longitude. Although the data are few they do show a definite trend. For four of the five longitudes, the catches were generally low in volume between 23° N. and 30° N., and moderately higher in volume between 30° N. and 37° N. in the region of the transition zone. Judging by the shape of the curves (fig. 14), we postulate that during this winter season the southern boundary of the transition zone may have occurred as far south as latitudes 30° N. to 32° N.

It would have been desirable to evaluate differences in the catch due to longitudinal variation using a two-way analysis of variance so as to separate variability due to latitude from that due to experimental error. Unfortuately, unequal groupings of observations along the various longitudes made this possible for only *Smith* cruises 30 and 31. Even for these two cruises some data collected at the extremities of several longitudinal sections could not be used owing to lack of corresponding data on adjacent sections. Also, in three instances, one of two values recorded close together along a longitude section was discarded in order that the analysis could be undertaken. The discarded values were determined by flipping a coin.

During *Smith* cruise 30, in July and August 1955, 6 or 8 night hauls were made with the 10-foot Isaacs-Kidd trawl on each of four longitudes, 180°, 172° W., 165° W., and 157° W., within the latitudinal range of 22° N. to 50° N. (fig. 15). As evaluated by a two-way analysis of variance, the differences in catch among longitudes were not significant ($F=3.09$; d.f.=3 and 15; $P>0.05$; F at the 0.05 level was 3.29). As for the 6-foot trawl (fig. 14), the catches taken on the northern portion of each section, in this case between 35° N.

and 50° N., averaged higher than those to the south. In this summer season it appears that the northern boundary of the transition zone occurred at about latitude 40° N., longitude 157° W., and then sloped to the south in a westerly direction.

Sampling with the 10-foot Isaacs-Kidd trawl was conducted on two cruises to the equatorial Pacific during which hauls were made along north-south sections. On *Smith* cruise 31, in October and November 1955, six or seven hauls were made at night on each of three longitudes, 140° W., 120° W., and 112° W., within the latitudinal range of 8° S. to 7° N. (fig. 16). In this case, as evaluated by a two-way analysis of variance, the differences among longitudes were significant ($F=6.81$; d.f.=2 and 10; $P<0.05$). Catches were generally higher in volume north of the Equator than south.

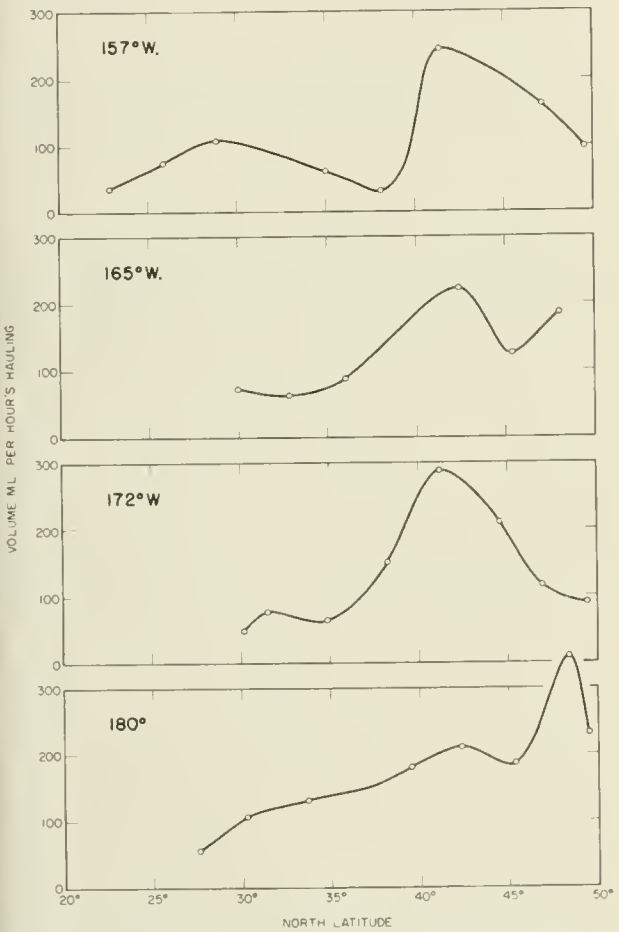

FIGURE 15.—Variation in trawl catch (volume in milliliters per hour of hauling) of the 10-foot Isaacs-Kidd trawl on four north-south sections, *Hugh M. Smith* cruise 30, July–August 1955.

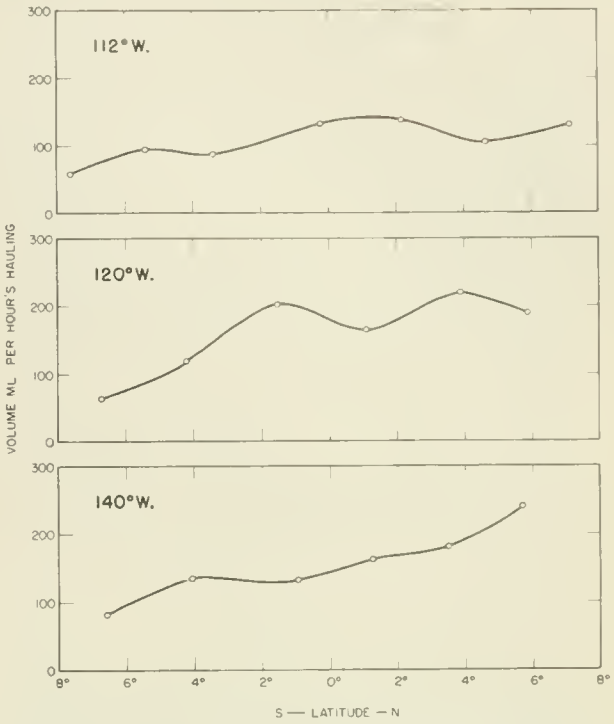

FIGURE 16.—Variation in trawl catch (volume in milliliters per hour of hauling) of the 10-foot Isaacs-Kidd trawl on three north-south sections, *Hugh M. Smith* cruise 31, October–November 1955.

During one part of cruise 31, hauls were made each night while the *Smith* was running generally to the east on a meandering course along the northern boundary of the Countercurrent. Volumes of the catches obtained on these hauls are plotted in figure 17 in relation to longitude and the position of the current boundary. There appears to be a doming or peaking in the volumes in the neighborhood of longitude 140° W. and again at 115° W. with a single high catch at 125° W. There is no apparent relation between volume of catch and distance north or south of the current boundary.

On *Smith* cruise 35, in August to October, 1956, 8 to 11 hauls were made on each of 4 longitudes, 160° W., 151° W., 143° W., and 135° W., within the latitudinal range of 20° S. to 11° N. (fig. 18). On three of the four sections, the peak volume occurred within 2° of the Equator. Although differences among longitudes were not significant ($F=0.37$; d.f.=3 and 32; $P>0.05$), there is indication of a trend in the region of the Equator

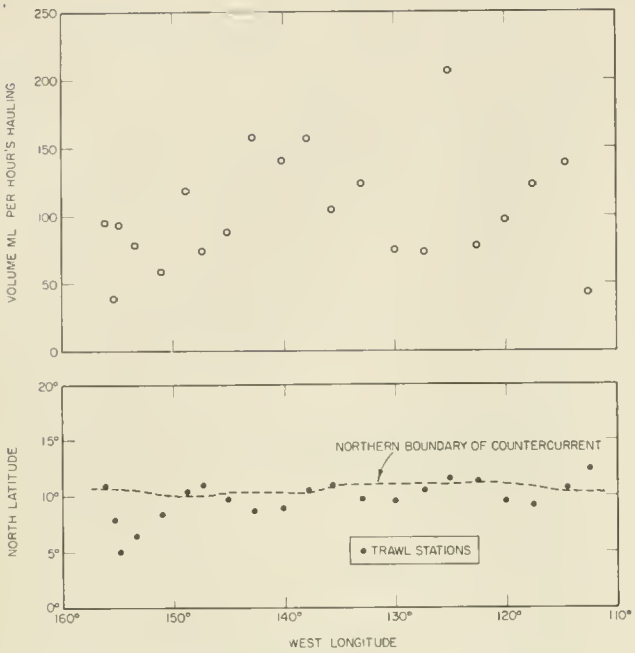

FIGURE 17.—Variation in trawl catch (volume in milliliters per hour of hauling), of the 10-foot Isaacs-Kidd trawl along the northern boundary of the Countercurrent, *Hugh M. Smith* cruise 31, September–October 1955.

with the catch volumes increasing to the westward between longitudes 135° W. and 151° W.

Austin and Rinkel (1958) have shown that there is an east-west variation in upwelling at the Equator with the maximum occurring in the eastern Pacific and the period of most active upwelling being August through October, which is the period of this cruise. King and Hida (1957a) found a gradient of decreasing zooplankton abundance along the Equator between longitudes 140° W. and 180°. Austin (1958) has shown that as the surface currents carry the newly upwelled water to the westward it "ages," i.e., it becomes warmer, its content of inorganic phosphate is reduced, and the thermocline deepens. We realize that the following explanation is an oversimplification of a very complex series of events, but we hypothesize that the reduction in the zooplankton standing crop to the west of 140° W. may be the result of heavy predation by an increasing population of forage organisms.

Differences between cruises.—The midwater trawling study was not conducted in a manner to permit the proper evaluation of differences related to seasons for any of the areas sampled. In three instances, however, an area was visited on two cruises at different times of the year, or in different years, which provided some comparison of differences between cruises that most likely were related to seasonal or annual changes in the environment.

The mean volumes obtained with the 6-foot Isaacs-Kidd trawl on *Manning* cruise 20 (April–May 1954) and *Manning* cruise 24 (March–April 1955) to the equatorial Pacific were not significantly different ($t=0.759$, $P>0.4$).

The catch volumes obtained with the 6-foot Isaacs-Kidd trawl on *Manning* cruise 22 (September–October 1954) and on *Smith* cruise 27 (January–February 1955) to the central North Pacific

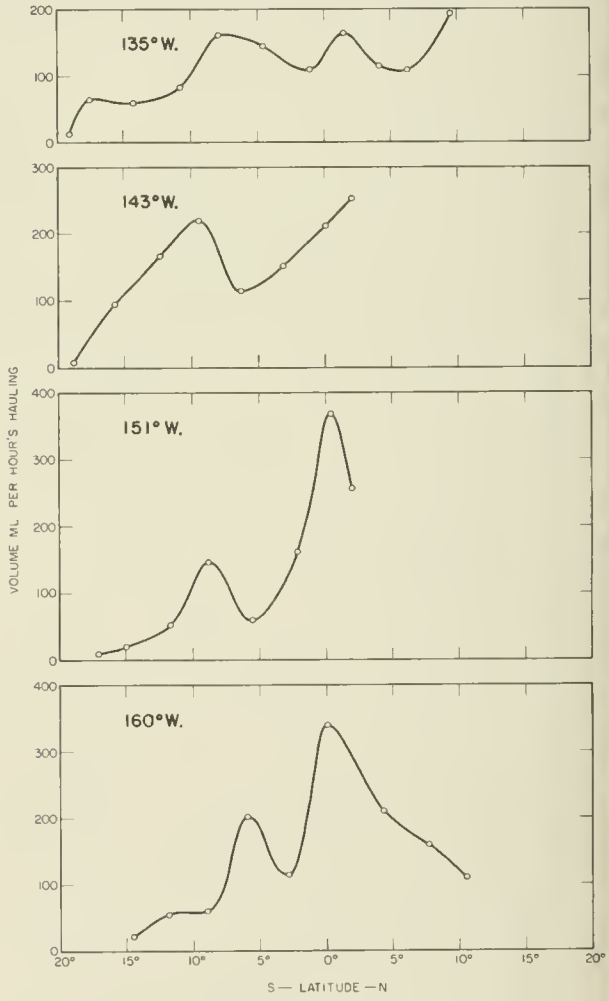

FIGURE 18.—Variation in trawl catch (volume in milliliters per hour of hauling) of the 10-foot Isaacs-Kidd trawl on four north-south sections, *Hugh M. Smith* cruise 35, August–October 1956.

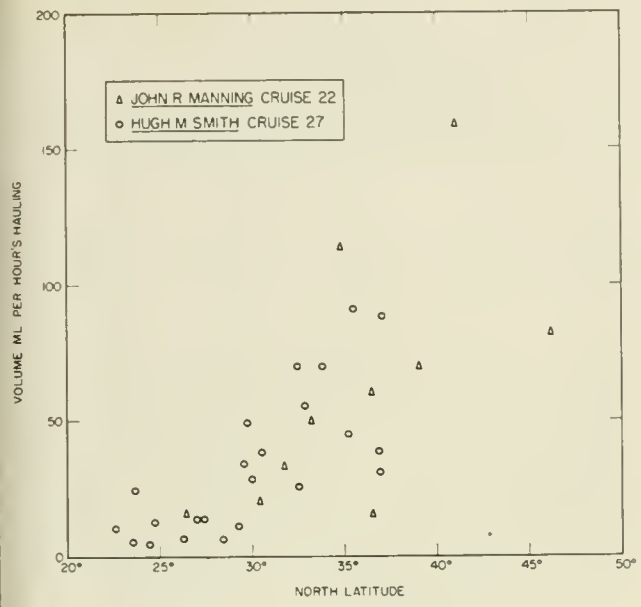

FIGURE 19.—Variation in trawl catch (volume in milliliters per hour of hauling) with latitude of the 6-foot Isaacs-Kidd trawl, *John R. Manning* cruise 22, September–October 1954, and *Hugh M. Smith* cruise 27, January–February 1955.

are plotted in figure 19. If the volumes north of 40° N., exclusively *Manning* cruise 22, and south of 25° N., exclusively *Smith* cruise 27, are omitted from the analysis, we find no significant difference ($t=0.614$, $P>0.5$) between cruises.

Employing the 10-foot trawl on *Smith* cruise 31 (September–December, 1955) and on *Smith* cruise 35 (August–October, 1956) to the equatorial Pacfic, we obtained catches with mean volumes not significantly different ($t=0.657$, $P>0.4$). Despite a wide variance in the data, there was a close similarity in the catch means when summarized by latitudinal zone (fig. 20).

On the basis of these simple "t" tests of the difference between means, we found in two instances no significant differences between cruises to the same general area at about the same time of year but in different years, and in a third instance no significant difference between two cruises to the same area but at different seasons (late summer and winter). These findings, together with those of the previous sections of this report, seem to indicate that the tropical marine fauna sampled by our midwater trawls is highly uniform in abundance both in space and time.

Variations in Composition of the Catch

It is evident from appendix tables 7 and 8 that there are north-south differences in the kinds and numbers of organisms captured by the Isaacs-Kidd trawls. These are summarized in a general manner in tables 14 and 15. We conclude that the largest number of categories of organisms was captured in the South Equatorial Current and in the Countercurrent (table 14); Hawaii and the North Pacific Current were next in rank; the poorest zones with respect to kinds of organisms were

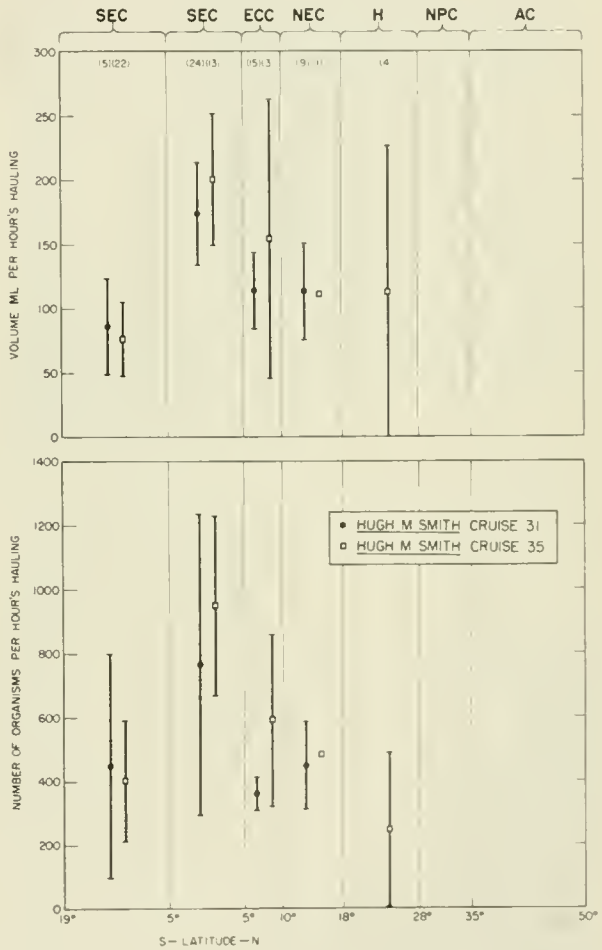

FIGURE 20.—Variation in trawl catch (volume in milliliters and number of organisms per hour of hauling) with latitude of the 10-foot Isaacs-Kidd trawl, *Hugh M. Smith* cruise 31, September–December, 1955, and *Hugh M. Smith* cruise 35, August–October, 1956. (Limits of the 0.95 fiducial interval are indicated for each mean. Number of hauls in each area is shown in parentheses.)

TABLE 14.—*Number of fish families and categories of organisms taken in the central Pacific, by trawl and latitude, 1953–56*

[Basic data in appendix tables 7 and 8; see p. 286 for description of faunal zones]

	SEC 20° S.–5° N.	ECC 5°–10° N.	NEC 10°–18° N.	Hawaii 18°–28° N.	NPC 28°–35° N.	AC 35°–50° N.	All areas
6-foot Isaacs-Kidd trawl:							
Number of samples	18	12	3	19	16	10	78
Number of fish families represented	17	17	7	16	16	8	33
Total number of categories, all forms	89	95	35	77	73	46	174
10-foot Isaacs-Kidd trawl:							
Number of samples	69	18	14	24	13	19	157
Number of fish families represented	36	25	18	30	15	15	53
Total number of categories, all forms	240	138	116	150	99	104	355

the North Equatorial Current and the Aleutian Current. As might be expected, this relation also holds true generally for the number of fish families represented in the catch. Although these data are variable, partly because there were more hauls in some areas than in others, they do show a general reduction in the variety of the fauna in a tropics-to-arctic direction, a well-known phenomenon (Hesse, Allee, and Schmidt, 1947: p. 24).

In table 15 we have attempted to classify the major groups of organisms according to their probable trophic level, based on information derived from a number of sources with MacGinitie and Mac Ginitie (1949) and Marshall (1954) being among the more useful. If we are not too greatly in error in our food-habit evaluations, it would appear that the Isaacs-Kidd trawls sample principally the primary carnivores, some of which are also herbivores and detritus feeders, such as the shrimps, and other animals which are secondary carnivores as well, such as the majority of the fishes. Very few, if any, of the fishes captured can be classed as herbivores.

TRAWL CATCHES AS ECOLOGICAL INDICATORS

The staff of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, has attempted to maintain an ecological approach in its investigations on the causes of variation in the abundance

TABLE 15.—*Major categories, probable trophic level, and latitudinal variation in abundance of organisms taken in the Isaacs-Kidd trawl catches, central Pacific, 1953–56*

Organisms	Probable trophic level			Occurrence and relative abundance [1]
	Herbivores and detritus feeders	Carnivores		
		Primary	Secondary	
Siphonophora		x		In all zones; abundant.
Medusae, unidentified		x		In all zones; numerous.
Ctenophora		x		In all zones; common.
Chaetognatha		x		In all zones; abundant.
Annelida	x(?)	x		In 4 zones; common.
Cirripedia	x(?)	x		In NPC and AC only; very abundant when present.
Mysidacea	x	x		Hawaii and south; few.
Amphipoda	x	x		In all zones; abundant.
Stomatopoda (larvae)		x		In 4 zones; common; not in NEC and AC.
Euphausiacea	x	x		In all zones; common to abundant; most abundant in NPC and AC.
Decapod Crustacea	x	x		In all zones; common to numerous; less abundant in NPC and AC.
Heteropoda	x			In all areas; common; more numerous in southern zones.
Pteropoda	x			In 5 zones; most numerous from Hawaii north.
Decapod Mollusca		x	x	In all zones; common; greatest variety in SEC.
Octopod Mollusca		x	x	In 4 zones; few.
Pyrosomatidae	x			In all zones; abundant; decreasing to the north.
Salpidae	x	x		In all zones; abundant.
Oonostomidae		x	x	In all zones; numerous; several species represented.
Sternoptychidae		x	x	In all zones; common.
Stomiatidae		x	x	In all zones; numerous; greatest variety of species in SEC.
Idiacanthidae		x	x	In all zones; common.
Paralepididae		x	x	In all zones; common.
Myctophidae		x	x	In all zones; abundant; greatest variety of species in SEC, fewest in NPC and AC.
Nemichthyidae		x	x	In all zones; common; most numerous in SEC and ECC.
Melamphaidae		x	x	In all zones; common.
Bramidae		x	x	In 3 zones; common; Hawaii and south.
Gempylidae		x	x	In 4 zones; common; not in NPC and AC.
Molidae		x		Only in SEC; few.
Leptocephali		x		In all areas; common.
Larval fish		x	x	In all areas; numerous.

[1] Faunal zones referred to are those indicated in appendix tables 7 and 8; see also p. 286.

and distribution of tunas. Studies have been pursued on the ocean currents, chemical nutrients, photosynthetic activity, zooplankton, and forage fish simultaneously with studies on the tunas. The trawling program has been conducted on the premise that highly mobile fishes, such as the tunas, are most likely to occur in areas with the most favorable concentrations of food. Other environmental factors, of course, such as temperature, can also be of a limiting nature and influence fish distribution. In general, however, when broad areas of the sea are being compared, it is our belief that a positive relation must exist among the various levels of the food chain. This does not mean that we expect to find a high positive correlation at all times and places between the volume of food and the abundance of tunas: in fact, it is possible that an inverse relation may exist locally after a period of heavy predation.

STANDING CROP AND PRODUCTIVITY MEASUREMENTS

Correlation analyses, made to investigate the association between trawl-catch volumes and environmental variables that might be expected to have some direct or indirect influence on the trawl catches, are summarized in table 16. For these analyses only data from the major cruises which were sufficient for meaningful statistical tests were employed.

On two of three cruises examined (*Smith* cruises 27 and 35), we found a significant ($P<0.01$) positive correlation of trawl volumes and surface inorganic phosphate concentrations; on the third cruise (*Smith* cruise 31) the relation was again positive but not significant ($P>0.05$).

Only two cruises (*Smith* cruises 31 and 35) provided estimates of photosynthetic activity based on the uptake of C^{14} by phytoplankton. Since the trawl hauls on these cruises were all made at night, at which time the photosynthetic activity was negligible, we also determined the correlation of trawl catch with the C^{14} uptake recorded at a station on the morning of the same day, and also with the C^{14} uptake measured at the station occupied on the morning following the night trawl haul. For both cruises the resulting correlation coefficients have positive values, but only those for *Smith* cruise 35, relating trawl catch to the rate of C^{14} uptake at the morning stations, were significant ($P<0.01$).

TABLE 16.—*Correlations of trawl catch (milliliters per hour of hauling), as the X_1 variate, with X_2 variate the surface inorganic phosphate, C^{14} uptake, or zooplankton volumes at the same station or from adjacent stations of the* Hugh M. Smith

Trawl and cruise	X_2 variate	Degrees of freedom	Correlation coefficient (r)	P
6-foot Isaacs-Kidd:				
Cruise 27	*Surface inorganic phosphate, μg. at./l.	21	0.665	<0.01
Do	†Zooplankton volumes, ml./1,000m.³; oblique 0–100 m. hauls.	21	0.617	<0.01
10-foot Isaacs-Kidd:				
Cruise 30	‡Zooplankton volumes, ml./1,000m.³; oblique 0–140 m. hauls.	35	0.701	<0.01
Cruise 31	§Surface inorganic phosphate, μg. at./l.	49	0.166	>0.05
Do	§Surface C^{14} uptake; mg. C/hr./m.³			
	a. Same station (1900–2000)	16	0.214	>0.05
	b. Adjoining station (0800–0900, same day).	28	0.198	>0.05
	c. Adjoining station (0800–0900, following day).	22	0.221	>0.05
Do	§Zooplankton volumes, ml./1,000m.³; oblique 0–200 m. hauls.	46	0.371	<0.01
Cruise 35	‖Surface inorganic phosphate, μg. at./l.	36	0.450	<0.01
Do	‖Surface C^{14} uptake, mg. C/hr./m.³			
	a. Same station (1900–2000).	36	0.237	>0.05
	b. Adjoining station (0800–9000, same day).	37	0.571	<0.01
	c. Adjoining station (0800–0900, following day).	36	0.581	<0.01
Do	‖Zooplankton volumes, ml./1,000m.³; oblique 0–140 m. hauls.	36	0.473	<0.01

* From McGary and Stroup (1958).
† Unpublished data in the files of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.
‡ From McGary, Jones, and Austin (1956).
§ From King, Austin, and Doty (1957).
‖ From Austin (1957).

In all four cruises examined (*Smith* cruises 27, 30, 31, and 35), the correlation between trawl-catch volume and zooplankton volume, as sampled on 0–100 m., 0–140 m., and 0–200 m. oblique hauls with 1-meter nets of silk or nylon grit gauze (aperture widths approximately 0.65 mm.), was found to be highly significant ($P<0.01$). It was certainly to be expected that the larger forage organisms sampled by the trawl would be found more closely related to zooplankton—their food for the greater part—than to inorganic phosphate or the metabolic activity of phytoplankton.

The distribution of the number and size of the organisms making up the different trophic levels, whether on land or in the sea, takes the form of a pyramid, with the plants or primary producers forming the broad base and the larger carnivores the peak (Odum, 1953: p. 73). Actually three ecological pyramids result from food and energy relationships: the pyramid of numbers, the pyramid of biomass, and the pyramid of energy or food

production rates. (Some ecologists consider the three—numbers, biomass, and energy—as different concepts of the same pyramid.) The concept of the pyramid of numbers was, perhaps, first given definite form by Elton (1927: p. 69). The pyramid of biomass was described for some Wisconsin lakes by Juday (1942) and similar studies have been made in other areas. The pyramid of production rates was introduced by Petersen (1918) in his calculations of the quantitative food relations in coastal waters where eelgrass, *Zostera* sp., is the main source of primary food. He postulated that 10 plant units were needed to produce 1 unit of herbivorous animal weight, and in turn, 10 herbivorous units were required for each unit weight of primary carnivore produced. The pyramid of energy, expressed in terms of efficiency or productivity rates for the various trophic levels, has been determined for lake environments by Lindeman (1942) and Juday (1942), and for a marine area—Georges Bank—by Clarke (1946).

A table of conversion factors, the pounds of feed needed to produce 1 pound of fish, is given in Brown (1957: vol. 1, p. 386); they range from 2.3 to 7.1 for various species. Petersen's 10× factor, however, is the one most frequently quoted.

The Honolulu Laboratory staff has obtained estimates of the biomass, or standing crop, at three trophic levels in the central Pacific: zooplankton, forage organisms, and tunas. Information on rate of production has also been obtained for the primary producers, i.e., the uptake of C^{14} by phytoplankton. Such data are not available for the other trophic levels but may be calculated from the information on hand.

Employing the data used in figure 13, we calculate that the average catch of the 6-foot trawl in 78 hauls was 1.86 ml./1,000 m.^{3} of water strained, and the average catch of the 10-foot trawl in 157 hauls was 1.65 ml./1,000 m.^{3}. For the same general area, zooplankton hauls averaged 29.64 ml./1,000 m.^{3}, or roughly 16 to 18 times the catch of the trawls. Although we are dealing with two standing-crop measurements, the relation is of the same order of magnitude as the 10× factor calculated by Petersen (1918) for the difference in production rate between two adjacent trophic levels.

Over the range of latitude sampled (49° N. to 19° S.), variations in zooplankton abundance were

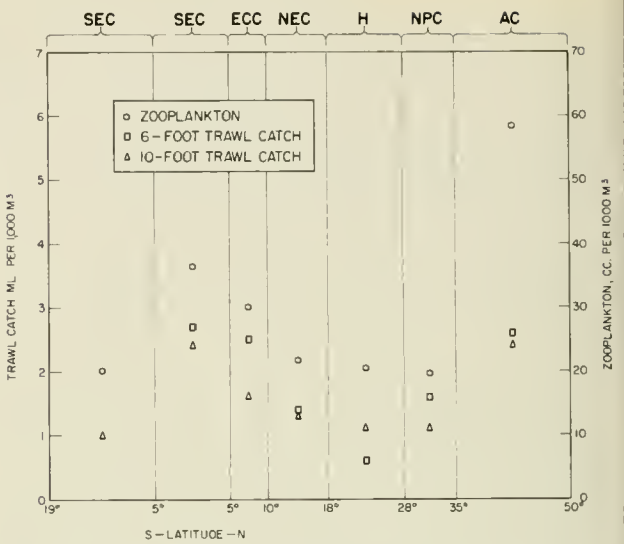

FIGURE 21.—Variation with latitude in the average volume of trawl catch per cubic meter of water strained by the 6- and 10-foot Isaacs-Kidd trawls, as compared with the zooplankton catch. (Zooplankton data for areas south of latitude 30° N. are from Kiug and Hida, 1957a and 1957b; for areas to the north of 30° N. from files of Bureau of Commercial Fisheries Biological Laboratory, Honolulu.)

closely paralleled by the trawl-catch volumes (fig. 21), except in the region of the Aleutian Current, where there was a marked increase in zooplankton catch that was proportionally much greater than the increase in trawl catch. Both measures of the fauna show the influence of enrichment in the region of the equatorial upwelling and to the north in the Aleutian Current.

Although the 6-foot trawl caught at a higher rate per unit of water strained than the 10-foot trawl in five of the six areas, the close correspondence in catch rates between the two trawls is of interest and provides further evidence that the trawls were about equal in efficiency. If the difference between the two trawls is of any significance, however, it may indicate that the larger net was sampling at a slightly different trophic level than the smaller net. This possibility is also indicated by the difference in size of organisms sampled by the two nets (table 7).

TRAWL CATCHES AS A MEASURE OF TUNA FOOD

One of the major aims of the midwater trawling program was to obtain a quantitative measure of the abundance and distribution of potential tuna food. Several reports have been published, others

are in press or in manuscript form, describing the food of tunas in the central Pacific (Welsh, 1949; Reintjes and King, 1953; King and Ikehara, 1956; Tester and Nakamura, 1957; Yuen, 1959; Nakamura, MS.;[3] Iversen, in press; and Waldron and King.[4]) These reports all emphasize the great variety of food that tunas consume, but point out certain differences related to the species and size of tuna and the depth, distance from land, season, and area of capture. Although adult tunas eat a number of organisms that might be classed as plankton (e.g., euphausiids, amphipods, and stomatopod and crab larvae), the bulk of their food consists of nekton, such as fishes, squids, and shrimps.

By means of the midwater trawl, we hoped to sample at a trophic level "closer" to the tunas than was possible with the 1-meter zooplankton nets. For this purpose, however, our procedures had a basic weakness: the trawls were operated almost entirely at night, since the catches were very poor during daylight hours, but our tuna fishing was carried out during the day because the few nighttime fishing stations had yielded very poor results. Therefore, the only comparison which our data afford is that between forage organisms captured at night and the stomach contents of tunas captured during the day. It would seem theoretically possible, however, as a result of the diurnal migration of the forage organisms, that the deep-swimming tunas caught in the daytime at depths of 100 to 500 feet may have been feeding on the same organisms that were taken at night in the trawl when it was fishing near the surface. Despite these basic differences in the data, we thought it worthwhile to make some general summaries and comparisons of trawl catch and tuna food, and also to examine station-to-station variations in these factors, as observed on certain cruises where both variables were evaluated.

In table 9 we summarized the number of taxonomic categories of organisms found in the trawl catches and in tuna stomachs. Although such a summary does not show the specific kinds of animals involved it does indicate that about twice as many phyla or subphyla were found in the trawl catches as were represented in the tuna stomachs. It is also evident, however, that a great variety of forms was found both in the trawl catches and in tuna stomachs.

An attempt is made in table 17 to illustrate the major differences and similarities in the composition of the trawl catches and of tuna stomach contents. Every item was listed that occurred in 10 percent or more of either the trawl collections or the stomachs of four species of tuna. Again, the data demonstrate the greater variety of organisms characteristic of the trawl catches, which seems to indicate that the tunas were not feeding at random but were exercising some degree of selection. The greatest similarity between the trawl catches and the tuna stomach contents was the occurrence in both of Amphipoda, *Phronima* sp., Stomatopoda, Euphausiidae, Decapoda (Crustacea and Mollusca), Enoploteuthidae, Salpidae, Tunicata, Stomiatidae, Paralepididae, Myctophidae, Gempylidae, and *Collybus drachme*. Some of the major differences were the high occurrence in the tuna stomachs of crab larvae, squids of the families Ommastrephidae and Loliginidae, and such fishes as *Gempylus serpens* and representatives of the families Bramidae and Acanthuridae, as contrasted with the low occurrence of these organisms in the trawl catches. On the other hand, it is evident from the table that a large number of animals of frequent occurrence in the trawl catches were not found in the tuna stomachs.

If the percentage of occurrence of the different taxonomic groups listed in table 17 for the Isaacs-Kidd trawls is plotted as a function of their occurrence in tuna stomachs, we obtain a series of distributions (fig. 22) which show, in 3 out of 10 instances, some indication of an inverse correlation. Organisms occurring with the highest frequency in the trawl collections were usually rare in the tuna stomachs, whereas those forms occurring most frequently in the tuna stomachs were not generally common in the trawl catches. (In fig. 22 we plotted points only for those organisms which occurred in both the tuna stomachs and the trawl catches.)

On a few cruises, tuna longline fishing and mid-

[3] Nakamura, E. L., MS. Food and feeding habits of Marquesan skipjack (*Katsuwonus pelamis*). Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

[4] Waldron, Kenneth D., and Joseph E. King. Food of skipjack in the central Pacific. U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Honolulu. (Experience Paper No. 26, Section No. 5, FAO World Scientific Meeting on the Biology of Tunas and Related Species, La Jolla, Calif.), July 1962.

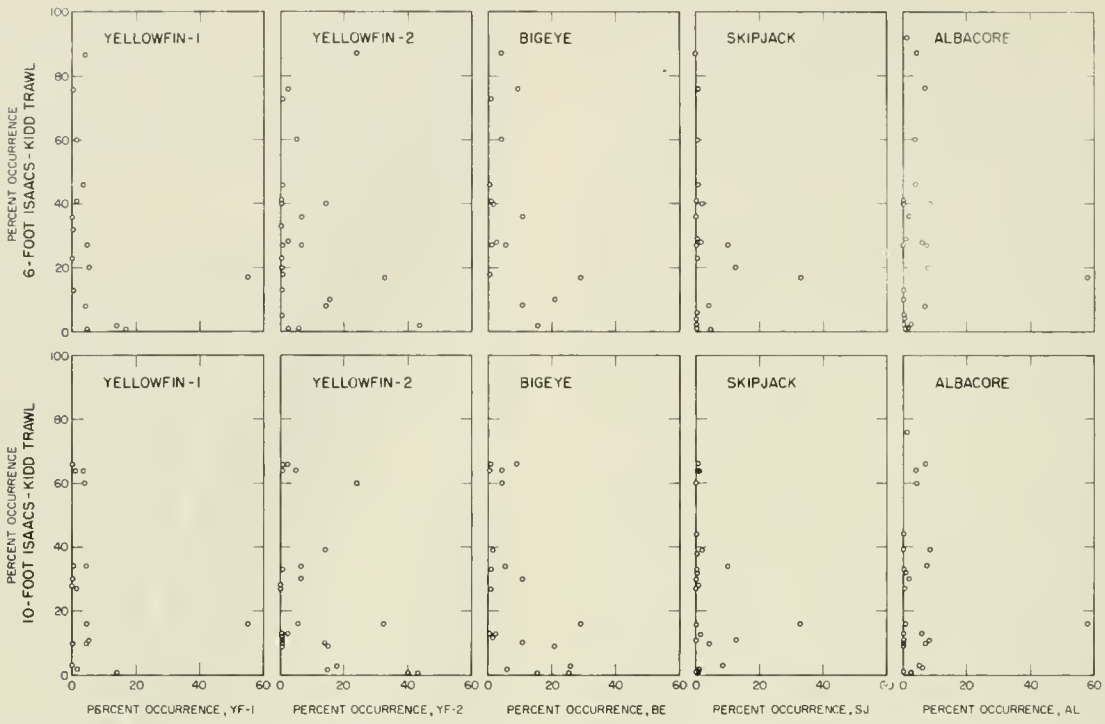

FIGURE 22.—Percentage occurrence of different taxonomic groups, listed in table 15, in the catches of the Isaacs-Kidd trawls and in tuna stomach contents. YF–1, yellowfin tuna, both surface dwelling and deep swimming; captured by live-bait fishing, surface trolling, and longline fishing (data from Reintjes and King, 1953). YF–2, yellowfin tuna, deep swimming; captured by longline fishing (data from King and Ikehara, 1956). BE, bigeye tuna, deep swimming; captured by longline fishing (data from King and Ikehara, 1956). SJ, skipjack tuna, both surface dwelling and deep swimming, captured by live-bait fishing, surface trolling, and longline fishing (unpublished data; see text, footnotes 3 and 4). AL, albacore tuna, both surface dwelling and deep swimming; captured by trolling and gill net and longline fishing (data from Iversen, in press).

TABLE 17.—*Percentage occurrence of all items identified in 10 percent or more of either the trawl collections or of tuna stomach contents*

Organism	In hauls of—				In stomach contents of—				
	6-foot beam trawl	1-meter ring trawl	6-foot Isaacs-Kidd trawl	10-foot Isaacs-Kidd trawl	Yellowfin [1]	Yellowfin [2]	Bigeye [2]	Skipjack [3]	Albacore [4]
Siphonophora	56	87	92	76					1.4
Medusae, unidentified	25	13	26	38					
Coelenterata, unidentified	44		4	20					
Ctenophora			8	13					
Chaetognatha	100	91	87	74					
Crustacea, unidentified	38	9	46	64	3.6	0.7	0.6	0.9	4.0
Copepoda	31	48	4	11				.1	.6
Idotheidae							10.0	7.2	.3
Amphipoda, unidentified	19	30	27	34	4.6	6.6	5.4	10.0	7.5
Phronima sp	25	9	40	39		14.1	1.8	2.1	8.6
Rhabdosoma sp	31	9	47	33					
Oxycephalus sp	25	13	29	32				.4	.9
Stomatopoda, unidentified	56	61	20	11	5.3	.5		12.6	8.0
Odontodactylus hanseni					12.9			.4	.3
Euphausiidae, unidentified	62	83	76	66	0.2	2.3	9.0	1.0	6.9
Thysanopoda monacantha			9	46					
T. tricuspidata	12		6	38				.6	
T. obtusifrons				11					
T. pectinata				15					
Nematobrachion flexipes			5	12					
Stylocheiron abbreviatum	6			15					
Sergestidae, unidentified	44	26	40						.3
Sergestes gardineri	19	4							
Sergestes sp	12		30	94					
Decapoda (Crustacea), unidentified	31	13	28	13		2.3	2.4	1.7	6.0
Gennadas scutatus	12		27	30					
G. propinquus				27					
G. tinayrei				10					

TABLE 17.—*Percentage occurrence of all items identified in 10 percent or more of either the trawl collections or of tuna stomach contents—Continued*

Organism	In hauls of—				In stomach contents of—				
	6-foot beam trawl	1-meter ring trawl	6-foot Isaacs-Kidd trawl	10-foot Isaacs-Kidd trawl	Yellowfin [1]	Yellowfin [2]	Bigeye [2]	Skipjack [2]	Albacore [4]
G. incertus				24					
Gennadas sp.	25	9	2	39					0.3
Funchalia taaningi	6		22	18					
Haplophorus typus	12		20	16					
H. gracilirostris	12		6	11					
H. foliaceus			15	25					
H. grimaldii	6		17	13					
Acanthephyra trispinosa	12	4	5	27					
Parapandalus zur strasseni	38	13	26	28					
Phyllosoma	6	9	13	10	0.5	0.5			.3
Crab larvae		13			48.2	7.1	0.6	13.3	.3
Heteropoda, unidentified			1	16	4.6	5.5		.1	.9
Pterotracheidae, unidentified	38	17	33			.2			
Pteropoda, unidentified	12	9	23	28	.1	.2		.4	
Corolla sp.			17						
Cymbuliidae, unidentified	12	4	20	7					
Decapoda (Mollusca), unidentified	19	26	17	16	55.0	32.6	28.9	33.0	58.0
Enoploteuthidae, unidentified	6		10	9		15.3	21.1		.3
Abraliopsis sp.			6	13					
Cranchiidae, unidentified	25	9	5	9		.5			.6
Ommastrephidae, unidentified				1		39.9	25.3	.7	.3
Loliginidae, unidentified						13.4	14.5	.9	4.9
Mollusca, unidentified	19		41	11					.3
Pyrosomatidae, unidentified	44	30	73	66		.9	1.2		
Salpidae, unidentified	44	52	87	60	3.9	24.1	4.2	.1	4.3
Iasis zonaria			6	16					
Tunicata, unidentified	44	35	41	27	1.5	.2	1.2	.1	.6
Gonostomidae, unidentified				10					
Gonostoma elongatum			15	19					
Gonostoma sp.	6			13					.3
Vinciguerria nimbaria			9	15					
V. lucetia	38	4	40	12		.5	1.8		
Vinciguerria sp.			4	34					
Diplophos taenia	31		5	7					
Argyropelecus aculeatus				20					
Thysanactis dentex			13	10					
Eustomias sp.	12		12	23					
Stomiatidae, unidentified	6	4	27	33		.9	1.2	.3	.3
Chauliodus sp.	6		1	29					
Idiacanthus sp.			1	23					
Paralepididae, unidentified		4	36	30	.1	6.4	10.8	.1	2.0
Scopelarchidae, unidentified				10					
Myctophidae, unidentified	56	9	60	64	1.5	4.8	4.2	.7	4.0
Hygophum reinhardti	6		19	1					
Hygophum sp.			1	16					
Benthosema sp.	12			1					
Myctophum evermanni	25		17	12					
M. brachygnathos	12			1					
M. spinosum	12			1					
M. aurolaternatum	12			1					
Notolynchnus valdiviae	19	9	9	5					
Diaphus sp.	50	4	41	44				.1	.3
Lampanyctus pyrsobolus	25		18	20					
L. macropterus				11					
Lampanyctus sp.	44	13	40	38					
Ceratoscopelus townsendi	38	4	24	31					
Cololabis sp.								.6	10.6
Nemichthys scolopaceus			10	20					
Serrivomer beani	12		1	3					
Bregmaceros macclellandi	2	4	18	13		.7	.6		
Melamphaidae, unidentified			2	23					
Howella sherborni				10					
Bramidae, unidentified				2	1.9	15.0	6.0	1.7	6.3
Collybus drachme		4	2	1	13.8	43.3	15.7	.3	2.6
Acanthuridae, unidentified	6		1		16.8	2.3		4.8	1.4
Oempylidae, unidentified			8	10	4.5	14.1	10.8	4.2	6.9
Gempylus serpens				3	.1	18.1	25.9	8.5	5.2
Leptocephali, unidentified	50	13	32	34	.5				
Heterosomata larvae	25								
Fish larvae	75	87	79						
Unidentified fish	44	22	29	86	48.2	48.5	48.8	30.7	34.2
Number of hauls or stomachs	16	23	78	157	1,097	439	166	707	348

[1] From Reintjes and King (1953).
[2] From King and Ikehara (1956).
[3] From Waldron and King (see footnote 4, p. 295).
[4] From Iversen (in press).

water trawling were conducted as a combined operation, with the longline being set in the early morning and hauled in the afternoon, and with a trawl haul usually being made about 2 hours after sunset on the run to the next fishing station. The data from *Manning* cruise 20 to the equatorial Pacific afford the best opportunity to compare, on a station-to-station basis, the composition of trawl catches obtained with the 6-foot Isaacs-Kidd and stomach contents of yellowfin tuna, *Neothunnus macropterus* (Temminck and Schlegel). The yellowfin captured on this cruise, from which stom-

achs were examined, ranged in size from 85 to 155 cm. (26 to 160 lb.) and averaged about 120 cm. (74 lb.). The fishing method, localities, and catch data for this cruise have been described by Iversen and Yoshida (1956).

Table 18 lists, for 16 days of cruise 20, the categories of organisms that comprised 1 percent or more, by volume, of the trawl catches and tuna stomach contents. Except for the first three stations (stations 1, 2, and 4), all the trawl hauls were made just after twilight or at night between 1840 and 2030 (zone time). It is obvious that whereas the trawl consistently caught such animals as siphonophores, chaetognaths, crustaceans, and tunicates, these organisms were largely missing from the tuna stomach contents. Decapod molluscs (squids), on the other hand, were prominent in tuna stomachs, but poorly sampled by the trawl. Among the families of fishes, the Thunnidae (*Katsuwonus pelamis*), Tetraodontidae, Molidae, Sternoptychidae, Bramidae, Nomeidae, and Balistidae were commonly found in the yellowfin stomachs but were not captured in any quantity by the trawl. Most of these families may be considered as pelagic fishes characteristic of the surface layer both in periods of light and darkness. For the Sternoptychidae, Marshall (1960) cites records of *Sternoptyx diaphana* being taken at 600–800 m., and *Argyropelecus hemigymnus* at 150–500 m. at night but below 500 m. during the day. The Myctophidae, Nemichthyidae, Gonostomidae, and Stomiatidae, which were the principal fishes captured in the trawl, are bathypelagic in distribution, occurring at the middepths during the day (Marshall, 1960: p. 82–88), but migrating to the surface layer at night. The virtual lack of these fishes in the food of yellowfin may indicate that this species feeds principally in the daytime and in the surface layer.

Some fishes, such as Thunnidae, Balistidae, and Gempylidae, commonly found in tuna stomachs, are strong, fast swimmers, and their absence from the trawl catches may simply indicate the ineffectiveness of the gear, and not that the tunas were particularly selective in their feeding, or that the trawl and the tunas were sampling different environments.

The results of two cruises to the central North Pacific, *Manning* cruises 22 and 23, provide an opportunity to compare the composition of trawl

TABLE 18.—*Percentage composition of the stomach contents of longline-caught yellowfin tuna and of the catches of the 6-foot Isaacs-Kidd trawl on* John R. Manning *cruise 20, equatorial Pacific, 1954*

Organisms [1]	Stomach contents	Trawl catch
May 17:		
Longline and trawl, station 1; 7 stomachs:		
Siphonophora		20
Chaetognatha		18
Amphipoda		41
Rhabdosoma sp		2
Octopoda	2	
Sepioteuthis sp	9	
Unidentified Decapoda (Mollusca)	15	
Tunicata		14
Katsuwonus pelamis	18	
Nomeidae	1	
Acanthuridae	1	
Ostraciidae	2	
Lactoria diaphanus	2	
Bramidae	3	
Ranzania laevis	33	
Apogonidae	3	
Leptocephali		2
Larval fish		2
Unidentified fish	11	
May 18:		
Longline and trawl, station 2; 3 stomachs:		
Siphonophora		1
Medusae		76
Chaetognatha		2
Amphipoda		16
Argonautidae	3	
Unidentified Decapoda (Mollusca)	8	
Salpidae		1
Katsuwonus pelamis	47	
Acanthuridae	6	
Collybus drachme	1	
Tetraodontidae	29	
Leptocephali		1
Larval fish		1
Unidentified fish	4	
May 19:		
Longline and trawl, station 4; 1 stomach:		
Siphonophora		46
Chaetognatha		6
Amphipoda		9
Phronima sp		6
Rhabdosoma sp		8
Unidentified Decapoda (Mollusca)	50	
Salpidae		21
Lactoria diaphanus	17	
Bramidae	17	
Larval fish		2
Unidentified fish	16	
May 22:		
Longline, station 8; trawl, station 9; 1 stomach:		
Siphonophora		2
Medusae		41
Euphausiacea		6
Octopodidae	58	
Argonautidae	25	
Pyrosomatidae		28
Salpidae		2
Lampanyctus sp		2
Photostomias sp		2
Eustomias sp		4
Thysanactis sp		9
Unidentified fish	16	
May 23:		
Longline, station 10; trawl, station 11; 7 stomachs:		
Siphonophora		5
Euphausiacea		5
Sergestes sp		2
Hoplophorus typus		2
Octopodidae	2	
Onycoteuthis banksii	4	
Unidentified Decapoda (Mollusca)	39	
Unidentified Tunicata		1
Pyrosomatidae		48
Salpidae		1
Isistius brasiliensis		16
Lactoria diaphanus	2	
Unidentified Bramidae	5	
Collybus drachme	6	
Anoplogaster cornutus	2	
Chauliodus sp		3
Nemichthys scolopaceus		2
Diaphus sp		4

[1] Includes all organisms or groups of organisms comprising 1 percent or more, by volume, of the stomach contents or of the trawl catches.

TABLE 18.—*Percentage composition of the stomach contents of longline-caught yellowfin tuna and of the catches of the 6-foot Isaacs-Kidd trawl on* John R. Manning *cruise 20, equatorial Pacific, 1954*—Continued

Organisms [1]	Stomach contents	Trawl catch
May 25:		
Longline, station 13; trawl, station 14; 8 stomachs:		
Siphonophora		26
Chaetognatha		2
Euphausiacea		6
Unidentified Decapoda (Crustacea)		3
Portunidae: Megalopa	8	
Funchalia taaningi		1
Sergestes sp		3
Hoplophorus typus		1
Unidentified Decapoda (Mollusca)	11	
Unidentified Tunicata		2
Pyrosomatidae		9
Salpidae		3
Trachypterus sp		8
Vinciguerria lucetia		15
Thysanactis dentex		5
Nemichthys scolopaceus		2
Diaphus sp		10
Cubiceps sp	9	
Nomeidae	25	
Acanthuridae	1	
Molidae	5	
Gempylus serpens	1	
Balistidae	29	
Unidentified fish	6	
May 26:		
Longline, station 15; trawl, station 16; 5 stomachs:		
Siphonophora		7
Chaetognatha		1
Euphausiacea		7
Unidentified Decapoda (Crustacea)	3	
Gennadas scutatus		1
Sergestes sp		1
Unidentified Decapoda (Mollusca)	14	
Vinciguerria lucetia		9
Echiostoma tanneri		16
Photostomias sp		2
Diaphus sp		7
Nomeidae	2	
Bramidae	18	
Gempylidae	2	
Paralepididae	2	
Balistes sp	17	
Balistidae	4	
Tetraodontidae	14	
Unidentified fish	23	
May 27:		
Longline, station 17; trawl, station 18; 10 stomachs:		
Siphonophora		5
Euphausiacea		2
Unidentified Amphipoda	6	
Phronima sp	3	
Gennadas scutatus		1
Sergestes sp		2
Hoplophorus typus		2
Unidentified Decapoda (Mollusca)	9	
Unidentified Tunicata	5	
Pyrosomatidae		69
Salpidae	1	
Photostomias sp		7
Thysanactis sp		3
Eustomias sp		2
Diaphus sp		2
Nomeidae	2	
Sternoptychidae	59	
Unidentified fish	13	
May 30:		
Longline, station 21; trawl, station 22; 12 stomachs:		
Siphonophora		13
Chaetognatha		2
Euphausiacea		6
Unidentified Decapoda (Crustacea)	2	
Hoplophorus foliaceus	6	
Funchalia taaningi		2
Sergestes sp		1
Portunidae: Megalopa	5	1
Unidentified Decapoda (Mollusca)	4	
Pyrosomatidae		18
Vinciguerria lucetia		36
Thysanactis dentex		2
Photostomias sp		1
Diaphus sp		12
Chaetodontidae	1	
Ranzania laevis	52	
Balistidae	2	
Tetraodontidae	6	
Sternoptychidae	14	
Paralepididae	5	
Unidentified fish	2	

TABLE 18.—*Percentage composition of the stomach contents of longline-caught yellowfin tuna and of the catches of the 6-foot Isaacs-Kidd trawl on* John R. Manning *cruise 20, equatorial Pacific, 1954*—Continued

Organisms [1]	Stomach contents	Trawl catch
May 31:		
Longline, station 23; trawl, station 24; 1 stomach:		
Siphonophora		22
Euphausiacea		13
Sergestidae		3
Funchalia taaningi		2
Unidentified Decapoda (Mollusca)	80	
Pyrosomatidae		21
Salpidae		7
Vinciguerria lucetia		1
Howella sp		6
Diaphus sp		10
Lampanyctus sp		3
Collybus drachme	17	
Larval fish		4
Unidentified fish	3	
June 1:		
Longline, station 25; trawl, station 26; 6 stomachs:		
Sergestes sp		2
Unidentified Decapoda (Mollusca)	12	
Pyrosomatidae		84
Salpidae		4
Aristostomias sp		2
Diaphus sp		1
Nomeidae	2	
Lactoria diaphanus	1	
Collybus drachme	2	
Ranzania laevis	58	
Gempylus serpens	6	
Tetraodontidae	1	
Remora remora	3	
Unidentified fish	10	
June 2:		
Longline, station 27; trawl, station 28; 5 stomachs:		
Siphonophora		15
Euphausiacea		16
Gennadas sp		3
Hoplophorus typus		3
Unidentified Decapoda (Mollusca)	48	
Pyrosomatidae		30
Salpidae		2
Nemichthys scolopaceus		3
Isistius brasiliensis		23
Vinciguerria lucetia		1
Collybus drachme	3	
Gempylidae	2	
Exocoetidae	16	
Paralepididae	3	
Tetraodontidae	11	
Sternoptychidae	2	
Unidentified fish	11	
June 3:		
Longline, station 29; trawl, station 30; 5 stomachs:		
Siphonophora		4
Euphausiacea		12
Gennadas scutatus		1
Sergestes orientalis		1
Heplophorus typus		3
Octopoda	4	
Unidentified Decapoda (Mollusca)	76	
Unidentified Tunicata	2	
Pyrosomatidae		20
Echiostoma tanneri		32
Bathophilus sp		1
Photostomias sp		1
Thysanactis sp		2
Bregmaceros macclellandi		2
Stomiatidae		9
Diaphus sp		4
Notolychnus valdiviae		1
Nomeidae	1	
Echeneidae	5	
Unidentified fish	9	
June 7:		
Longline, station 33; trawl, station 34; 5 stomachs:		
Siphonophora		14
Chaetognatha		2
Euphausiacea		26
Unidentified Decapoda (Crustacea)		1
Unidentified Crustacea	1	
Funchalia taaningi		5
Sergestes sp		2
Hoplophorus foliaceus		3
H. typus		2
Enoplometopus sp	2	
Portunidae: Megalopa	1	
Unidentified Decapoda (Mollusca)	2	
Enoploteuthidae		4
Pyrosomatidae		16
Diaphus sp		13

TABLE 18.—*Percentage composition of the stomach contents of longline-caught yellowfin tuna and of the catches of the 6-foot Isaacs-Kidd trawl on* John R. Manning *cruise 20, equatorial Pacific, 1954*—Continued

Organisms [1]	Stomach contents	Trawl catch
June 7—Con.:		
Myctophum evermanni		2
Acanthuridae	5	
Collybus drachme	3	
Bramidae	2	
Tetraodontidae	58	
Balistidae	1	
Echeneidae	6	
Exocoetidae	7	
Larval fish		2
Unidentified fish	9	
June 9:		
Longline, station 36; trawl, station 37: 3 stomachs:		
Siphonophora		8
Odontodactylus sp	1	
Euphausiacea		19
Funchalia taaningi		2
Sergestes sp		9
Hoplophorus typus		4
H. foliaceus		2
Unidentified Decapoda (Mollusca)	6	
Liocranchia reinhardti		8
Unidentified Tunicata		2
Pyrosomatidae		9
Salpidae		1
Astronesthes sp		2
Echiostoma tanneri		10
Photostomias sp		2
Diaphus sp		10
Hygophum reinhardti		2
Lampanyctus pyrsobolus		2
Myctophidae		2
Nomeidae	3	
Acanthuridae	5	
Ranzania laevis	76	
Balistidae	2	
Larval fish		3
Unidentified fish	4	
June 10:		
Longline, station 38; trawl station 39; 2 stomachs:		
Siphonophora		13
Euphausiacea		16
Sergestes orientalis		1
Argonautidae	1	
Unidentified Decapoda (Mollusca)	12	
Unidentified Tunicata	1	
Pyrosomatidae		31
Salpidae		2
Vinciguerria lucetia		7
Ceratoscopelus townsendi		4
Lampanyctus sp		1
Unidentified Myctophidae		1
Diaphus sp		16
Katsuwonus pelamis	84	
Larval fish		2
Unidentified fish	1	

[1] Includes all organisms or groups of organisms comprising 1 percent or more, by volume, of the stomach contents or of the trawl catches.

catches obtained with the 6-foot Isaacs-Kidd trawl with the stomach contents of albacore tuna, *Thunnus germo* (Lacépède), captured by longline. The fishing method, localities, and catch data for these cruises are described by Shomura and Otsu (1956). The 10 albacore stomachs preserved on *Manning* cruise 22 were from fish averaging 73.3 cm. in fork length, whereas the 14 stomachs preserved on *Manning* cruise 23 were from fish averaging 101.2 cm. All trawl hauls were made at night between 1900 and 2030 hours.

Although the data are sparse and do not permit a station-to-station comparison, when summarized over the entire cruise as in tables 19 and 20, they show certain major features in common with the yellowfin stomach contents-trawl catch comparison (table 18). Coelenterates and crustaceans made up important percentages of the volume of the trawl catches but, except for Amphipoda (cruise 23), were relatively insignificant in the stomach contents. Of the Mollusca, Pteropoda were of some importance in the trawl collections whereas Cephalopoda were largely missing; this situation was just reversed in the albacore food, where Pteropoda were absent and Cephalopoda were very important. Among the Tunicata, the Pyrosomatidae were an important part of the

TABLE 19.—*Percentage composition of stomach contents of 10 albacore taken by longline and of catches of the 6-foot Isaacs-Kidd trawl,* Manning *cruise 22, central Pacific, September–October 1954*

Organisms [1]	Stomach contents	Trawl catch
Siphonophora		4
Unidentified Medusae		5
Lepas fascicularis (larvae)		10
Lepas sp		5
Phronimidae	1	
Unidentified Euphausiidae	1	20
Thysanopoda sp		2
Funchalia taaningi		1
Hoplophorus grimaldii		4
Unidentified Sergestidae		5
Unidentified Crustacea		4
Unidentified Pteropoda		1
Corolla sp		3
Unidentified Decapoda	7	
Abraliopsis sp		1
Pyrosomatidae		15
Salpidae	2	2
Unidentified Myctophidae		8
Tarletonbeania sp	40	
Scomberesocidae:		
Cololabis sp	46	
Total	97	90

[1] Includes all organisms or groups of organisms comprising 1 percent or more, by volume, of the stomach contents or of the trawl catches.

TABLE 20.—*Percentage composition of stomach contents of 14 albacore caught by longline and of the catches of 3 trawl hauls made with the 6-foot Isaacs-Kidd trawl,* John R. Manning *cruise 23, central North Pacific, December 1954*

Organisms [1]	Stomach contents	Trawl catch
Siphonophora		4
Unidentified Medusae		1
Chaetognatha		2
Annelida		1
Unidentified Amphipoda	4	
Unidentified Crustacea		12
Unidentified Decapoda	25	1
Onycoteuthidae	14	
Argonautidae	3	
Unidentified Cephalopoda	1	
Pyrosomatidae		32
Salpidae	3	40
Sternoptychidae	3	
Alepisaurus sp	2	
Unidentified Myctophidae		1
Lampadena sp		3
Cololabis sp	35	
Unidentified Pisces	8	
Total	98	97

[1] Includes all organisms or groups of organisms comprising 1 percent or more, by volume, of the stomach contents or of the trawl catches.

TABLE 21.—*Collection data for six juvenile tuna captured by midwater trawl in the central Pacific, 1952–56*

Number of juveniles	Species	Total length	Gear of capture	Depth of haul	Vessel and cruise	Date taken	Time taken	Station No.	Position	
									Latitude	Longitude
		Millimeters		*Meters*			*Zone time*			
1	*Katsuwonus pelamis*	18	6-ft. beam	0–103	*Hugh M. Smith*—15	June 21–22, 1952	2235–0015	62–1	5°56′ N.	139°26′ W.
1	do	18	1-m. ring	0–187	*Charles H. Gilbert*—11.	Apr. 9, 1953	0212–0314	12–D	20°35′ N.	157°32′ W.
1	Unidentified	<20	6-ft. Isaacs-Kidd	0–95	*John R. Manning*—20.	June 3, 1954	1842–1957	30	1°44′N.	158°15′ W.
2	do	20 60	10-ft. Isaacs-Kidd	0–118	*Hugh M. Smith*—27	Feb. 1, 1955	1939–2041	25–1	29°56′ N.	179°28′ E.
1	*Katsuwonus pelamis*	22	do	0–176	*Hugh M. Smith*—35	Sept. 26, 1956	1905–2005	165	0°02′ N.	159°50′ W.

trawl catches and the Salpidae were present in lesser volume; in the tuna food the Pyrosomatidae were lacking, but the Salpidae were present in about the same volume as in the trawl samples. Sauries (*Cololabis* sp.), the largest single item in the albacore stomachs examined, were not taken in the 6-foot Isaacs-Kidd trawl. On cruise 22, a lanternfish (*Tarletonbeania* sp.) ranked large in volume in the albacore food, but was not taken in the trawl. Other kinds of lanternfish were captured in the trawl on cruise 23, however, that did not occur in the tuna stomachs.

On the basis of these data we conclude that the 6-foot Isaacs-Kidd trawl did not sample the immediate food of yellowfin and albacore tuna in the equatorial Pacific and central North Pacific. With respect to the food of other tuna species, such as bigeye (*Parathunnus sibi*) and skipjack (*Katsuwonus pelamis*), we do not have sufficient information collected concurrently with midwater trawl catches to provide within-cruise or station-to-station comparisons. For these species our best data are those given in table 17 and figure 22.

MIDWATER TRAWLS AS SAMPLING DEVICES FOR JUVENILE TUNAS

Larval tunas of several species have been captured in the central Pacific in 1-meter zooplankton nets with mesh apertures about 0.65 mm. in width (Matsumoto, 1958; Strasburg, 1960). The young tunas captured in this manner have ranged from 3 to about 12 mm. in length, but specimens larger than 6 mm. were uncommon in the catch. The number captured per 30-minute haul has varied from none to several hundred. Both of these authors concluded that diurnal differences in the catch of tuna larvae resulted primarily from vertical migrations and only secondarily from the increased ability of the larvae to dodge the net during the daytime.

The almost complete absence from the plankton catches of young tuna more than 12 mm. in length (Strasburg, 1960) could possibly be attributed to their living in a different habitat or level of the sea than that sampled by the plankton nets or to their ability to dodge the net. Since the plankton net sampled the mixed layer and usually beyond, to depths as great as 200 meters and sometimes greater, and the hauls were spaced over a wide range of latitude and longitude at all seasons of the year, it would seem reasonable to believe that the environment occupied by the young tunas was being sampled, but at sizes above 12 mm. they easily escaped the 1-meter net.

It was our hope that by means of midwater trawls we would capture juvenile tunas of lengths above 12 mm. which were able to elude the plankton nets. In 274 hauls made with the four midwater trawls described in this report we captured only six juvenile tunas, which ranged from 18 to 60 mm. in length. Three of the six were caught in the 10-foot Isaacs-Kidd trawl; the remainder were taken in the other three trawls. The collection data for these six specimens are given in table 21.

On cruise 15 of the *Smith*, 7 yellowfin, 36 skipjack, and 13 unidentified tuna larvae were captured in hauls of 1-meter zooplankton nets between latitude 6° N. and the Equator along longitude 140° W. (Matsumoto, 1958). Four hauls with the 6-foot beam trawl made in this area on cruise 15 yielded only 1 juvenile tuna, a skipjack (*Katsuwonus pelamis*) 18 mm. in length (table 21). There was evidence, therefore, that considerable numbers of larval tunas, and most likely juvenile tunas, were in the area but were not captured by the beam trawl. We expected the larvae to escape through the relatively coarse meshes of the trawl

net, but we did hope to retain the juveniles 20 mm. and larger.

The plankton collections obtained on the other four cruises cited in table 21, on which one or two juvenile tunas were taken in midwater trawls, have not yet been sorted for larval tunas. From our knowledge of the widespread occurrence of the larvae (Matsumoto, 1958), however, and of the distribution of the adults, we believe that juvenile tunas were present in the areas sampled. Our failure to catch them in larger quantities indicates the ineffectiveness of our gear for sampling this portion of the fauna.

SUMMARY

This study is based on the quantitative analysis of the catches from 274 midwater-trawl hauls made on 22 cruises of Bureau of Commercial Fisheries vessels in the central Pacific Ocean between latitudes 49° N. and 19° S., and longitudes 108° W. and 162° E., during the years 1951 to 1956.

Chief purpose of the trawling program was to obtain quantitative estimates of the abundance and distribution of forage organisms, particularly those utilized by tunas.

Four types of trawls were employed: 6-foot beam trawl, 1-meter ring trawl, and 6-foot and 10-foot Isaacs-Kidd trawls. Descriptions and specifications of the four trawls are provided. Hauls were usually of the double oblique type with the net fishing between the surface and depths as great as 400 meters.

In the laboratory, the catch was sorted and the different kinds of organisms identified to the most precise degree considered practical. The number and displacement volume were determined for each kind or group of organisms identified.

Volume of the catch varied generally with size of the trawl. In terms of volume of catch per unit of mouth area, the trawls were about equal in catching efficiency within a geographical area. Essentially, all four trawls sampled organisms from the same phyla, classes, and orders, but differed in the families and genera of fishes they sampled—the largest and most frequently used trawls caught the greatest variety of organisms.

Night catches greatly exceeded day catches both in volume and number of organisms, and also yielded organisms of larger size. Marked diurnal differences were noted in the composition of the trawl catches. Coelenterates, amphipods, stomatopod larvae, certain molluscs, and tunicates occurred in about equal frequency in day and night collections, whereas the faster-swimming forms, such as the decapod Crustacea, squids, and most of the fishes, were taken principally at night. We believe that the day/night difference in catch was due largely to a diurnal migration and the movement of the organisms into the surface layer at night, rather than to an ability to dodge the net during the day.

With respect to geographic variation, catches of the Isaacs-Kidd trawls showed two peaks in abundance: in the Aleutian Current and in the region of upwelling and enrichment at the Equator. The poorest catches were made in the South Equatorial Current south of 5° S. latitude, in the North Equatorial Current between 10° N. and 18° N. latitude, and in Hawaiian waters. Evaluation by a two-way analysis of variance indicated differences ($P<0.05$) among longitudes in the volume of trawl catches made with the 10-foot Isaacs-Kidd trawl during one cruise to the equatorial Pacific.

On the basis of "t" tests of the difference between mean catch volumes, we found no significant differences between cruises to the same general area (equatorial Pacific) at about the same time of year, or to the same area (central North Pacific) at different seasons (late summer and winter).

In correlation analyses of the relation of trawl catch volumes and various environmental factors, we found a significant ($P<0.01$) positive correlation of trawl volumes and surface inorganic phosphate for two cruises and a positive but not significant ($P>0.05$) relation for a third cruise. On one cruise the relation of trawl volumes to C^{14} uptake by phytoplankton was positive but nonsignificant ($P>0.05$), whereas on a second cruise the correlation coefficient was significant ($P<0.01$). On all four cruises studied, the correlation between zooplankton volumes and trawl catches was found to be significant ($P<0.01$). These results were in line with our expectations: that the forage organisms would be more closely related to zooplankton—their food for the greater part—than to inorganic phosphate or the metabolic activity of phytoplankton.

Expressing the catch in terms of volume per unit volume of water strained, we obtained an average catch for the 6-foot Isaacs-Kidd trawl of 1.86 ml./1,000 m.^{3}, and an average of 1.65 ml./1,000 m.^{3} for the 10-foot Isaacs-Kidd trawl. These volumes are approximately one-sixteenth to one-eighteenth of the average zooplankton volume obtained for the same general area.

A much greater variety of organisms was found in the trawl catches than in the tuna stomachs, which might indicate some degree of selection by the tunas. Most fishes in tuna stomachs were pelagic—characteristic of the surface layer during both day and night. The most abundant fishes in the trawl catches were bathypelagic, occurring in the middepths during the day and migrating to the surface layer at night. A virtual lack of these fishes in the tuna stomachs examined may indicate that tunas feed principally in the daytime and in the surface layer. Since the trawls were operated almost entirely at night because the catches were very poor during daylight and tuna fishing was carried out during the day, it was not too surprising to find a very poor correspondence between the composition of the trawl catches and the contents of tuna stomachs, with the similarities greatly outweighed by the differences.

In 274 hauls made with the 4 types of trawls we caught only 6 juvenile tunas, ranging in length from 18 to 60 mm. On the basis of catches of larval tunas made in zooplankton nets and our knowledge of the distribution of the adults, we believe juvenile tunas were present in these areas at the time of the trawling.

The greatest variety of organisms was captured in the South Equatorial Current and in the Countercurrent, the poorest variety in the North Equatorial Current and Aleutian Current. Midwater trawls sampled principally primary and secondary carnivores, some of which may also be classed as herbivores and detritus eaters. Strictly herbivorous animals were very scarce in the catches.

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APPENDIX TABLE 1.—*Summary of collection of organisms with 6-foot beam trawl, by cruise, central Pacific, 1951 and 1952*

Station	Position		Date	Start of haul	Length of haul	Estimated maximum depth	Catch/hour haul			Unusually numerous or bulky organisms	
	Latitude	Longitude					Number	Volume	Adjusted volume [1]	Number	Volume
John R. Manning:			*1951*	*Zone time*	*Hours*	*Meters*		*Milliliters*	*Milliliters*		*Milliliters*
Cruise 9:											
17	21°26.4′ N.	158°12.5′ W.	Nov. 26	1200	1.07	44	7	1.3			
18	21°26′ N.	158°13.5′ W.	Nov. 26	1410	.88	156	131	8.0			
19	21°24.5′ N.	158°16.3′ W.	Nov. 26	1525	.97	182	126	5.3			
20	21°21.8′ N.	158°21.1′ W.	Nov. 26	1704	1.02	175	228	19.8			
21	21°26.4′ N.	158°12.5′ W.	Nov. 26	1947	.93	25	112	5.9			
22	21°26′ N.	158°13.5′ W.	Nov. 26	2101	1.07	169	80	20.6			
23	21°24.5′ N.	158°16.3′ W.	Nov. 26	2233	1.05	169	159	77.1			
24A	21 21.8′ N.	158°21.1′ W.	Nov. 27	0021	1.00	200	184	51.0			
24B	21°21.8′ N.	158°21.1′ W.	Nov. 27	0204	2.27	450	154	31.4	18.6	1 Scyphozoa	29.0
27	21°23.1′ N.	158°12.5′ W.	Nov. 27	1040	.58	200	117	4.0			
Hugh M. Smith:			*1952*								
Cruise 14:											
14	04°58′ S.	155°00′ W.	Feb. 1	1923	.33	5	106	13.0			
16	06°50′ S.	155°05′ W.	Feb. 2	1412	.33	5	82	1.2			
Cruise 15:											
61-1	06°00′ N.	139°57′ W.	June 20	2301	1.48	300	1,695	83.4		1,000 euphausiids	18.0
61-2	06°00′ N.	139°54′ W.	June 21	0040	1.83	103	14,310	434.0		25,000 euphausiids	613.4
62-1	05°56′ N.	139°26′ W.	June 21	2235	1.67	103	2,062	217.2		1,000 euphausiids	48.4
62-2	05°56′ N.	139°23′ W.	June 22	0035	2.40	219	1,146	136.9		720 euphausiids	37.8

[1] Total catch per hour less unusually large organisms or "jellies" constituting 50 percent or more of the catch.

APPENDIX TABLE 2.—*Summary of collection of organisms with 1-meter ring trawl, by cruise, central Pacific, 1953*

Station	Position		Date	Start of haul	Length of haul	Estimated maximum depth	Catch/hour haul	
	Latitude	Longitude					Number	Volume
Charles H. Gilbert:				*Zone time*	*Hours*	*Meters*		*Milliliters*
Cruise 11:								
5A	21°49.3′ N.	157°32.2′ W.	April 1	1405	1.65	200	14	1.3
8D	20°35.1′ N.	157°32′ W.	2	0224	1.03	200	134	6.3
9A	21°49.3′ N.	157°32.4′ W.	8	1330	1.00	134	54	2.3
12D	20°34.9′ N.	157°32.3′ W.	9	0212	1.03	187	83	11.6
13A	21°49.9′ N.	157°32.1′ W.	14	1307	1.18	198	31	5.3
16D	20°35.2′ N.	157°32′ W.	15	0234	1.02	198	136	6.9
17A	21°48.8′ N.	157°32′ W.	22	1310	1.12	144	50	2.5
20D	20°35.2′ N.	157°32′ W.	23	0202	.98	165	167	14.2
21A	21°50.7′ N.	157°31′ W.	29	1248	.98	227	58	1.9
24D	20°35′ N.	157°32′ W.	30	0410	1.08	196	94	3.8
Cruise 12:								
1A	21°50′ N.	157°32′ W.	May 8	1505	1.25	200	81	0.9
4D	20°35.2′ N.	157°32′ W.	9	0250	.92	199	25	9.6
13A-1	21°50′ N.	157°32′ W.	14	1320	1.08	134	16	0.6
13A-2	21°50′ N.	157°32′ W.	14	1430	1.00	171	154	2.8
16D-1	20°35′ N.	157°32′ W.	15	0225	1.10	118	141	9.7
16D-2	20°35′ N.	157°32′ W.	15	0335	1.00	171	54	27.6
16D-3	20°35′ N.	157°32′ W.	15	0440	1.08	169	157	6.9
17A-1	21°49.8′ N.	157°32′ W.	28	1440	1.25	193	25	0.4
17A-2	21°49.8′ N.	157°32′ W.	28	1602	.83	206	26	1.1
20D	20°35.2′ N.	157°32.2′ W.	29	0510	1.18	168	32	0.7
Cruise 13:								
1A	21°50′ N.	157°32′ W.	June 4	1550	1.25	155	7	1.1
4D	20°35.3′ N.	157°32.3′ W.	5	0340	1.17	169	4	1.8
Hugh M. Smith:								
Cruise 21:								
23	23°10′ N.	159°21.2′ W.	Aug. 10	2140	1.25	90	14	5.7

APPENDIX TABLE 3.—*Summary of collection of organisms with 6-foot Isaacs-Kidd trawl, by cruise, central Pacific, 1953–55*

Station	Position		Date	Start of haul	Length of haul	Estimated maximum depth	Catch/hour haul			Unusually numerous or bulky organisms	
	Latitude	Longitude					Number	Volume	Adjusted volume [1]	Number	Volume
John R. Manning;			*1953*	*Zone time*	*Hours*	*Meters*		*Milliliters*	*Milliliters*		*Milliliters*
Cruise 15:											
4	08°23′ N.	150°12′ W.	May 4	1930	1.00	200	129	93.1			
Cruise 16:											
Test	21°05′ N.	157°58′ W.	July 21	0853	1.32	169	39	8.0			
5	08°27′ N.	154°48.6′ W.	July 30	1930	1.27	200	346	136.8			
7	07°04.2′ N.	154°55.1′ W.	July 31	1935	1.35	200	381	110.1			
Cruise 20:			*1954*								
Test 1	21°40′ N.	158°09′ W.	Apr. 28	1900	.33	15	264	10.0			
Test 2	21°39.5′ N.	158°10.3′ W.	Apr. 28	1931	.60	230	250	35.7			
Test 3	21°00.5′ N.	157°49′ W.	Apr 29	0713	1.25	135	122	7.5			
Test 4	21°56′ N.	157°49′ W.	Apr. 29	0838	.93	232	90	4.2			
1	05°58′ N.	162°52.5′ W.	May 17	0755	1.38	110	170	3.2			
2	05°59′ N.	162°28′ W.	May 18	0712	1.33	110	260	16.1			
4	06°05′ N.	162°18′ W.	May 19	0650	1.27	100	161	5.3			
5	05°58′ N.	161°53′ W.	May 20	0710	1.22	100	41	20.9			
7	05°49′ N.	161°03.9′ W.	May 21	1848	1.17	90	631	67.4			
9	05°18.5′ N.	161°29′ W.	May 22	1855	1.30	100	597	145.3	49.2	23 medusae 22 tunicates	78.0 47.0
11	04°46.5′ N.	161°03.5 W.	May 23	1847	1.38	100	1,086	114.6	59.5	33 tunicates	76.0
14	04°41′ N.	159°53′ W.	May 25	1850	1.30	90	867	111.8			
16	04°36.5′ N.	159°41′ W.	May 26	1843	1.28	85	962	126.2	77.7	44 tunicates	62.0
18	04°07.5′ N.	160°12.4′ W.	May 27	1846	1.28	100	523	163.3	50.0	38 tunicates	145.0
22	03°53.2′ N.	158°47.8′ W.	May 30	1842	1.25	100	2,042	79.0			
24	03°53.2′ N.	158°23′ W.	May 31	1842	1.28	95	756	67.3			507.0
26	02°47.1′ N.	158°55.4′ W.	June 1	1845	1.45	90	323	415.6	65.9	36 tunicates	507.0
28	02°09′ N.	158°16.5′ W.	June 2	1842	1.27	95	475	104.7			
30	01°43.9′ N.	158°14.9′ W.	June 3	1842	1.25	95	574	99.8		1 fish	40.0
34	01°48.5′ N.	156°54.9′ W.	June 7	1840	1.27	90	806	66.8			
37	01°26′ N.	158°18.8′ W.	June 9	1840	1.28	85	594	42.4			
39	00°38.4′ N.	158°48′ W.	June 10	1844	1.30	90	736	47.4			
Cruise 21:											
2	20°42′ N.	157°14.5′ W.	July 23	2016	1.35	187	181	30.4			
4	19°36.5′ N.	157°32.5′ W.	July 25	1913	1.23	144	141	55.2			
6	19°35.4′ N.	157°21′ W.	July 26	2008	1.23	136	85	10.2			
9	20°45′ N.	157°15′ W.	July 28	2011	1.40	209	174	17.1			
Cruise 22:											
2	26°24.5′ N.	159°14.2′ W.	Sept. 15	1924	1.05	105	341	37.8	16.1	6 tunicates	22.8
4	30°25.1′ N.	159°57.5′ W.	Sept. 17	1910	1.05	95	2,328	36.5	20.3	5 tunicates	17.0
6	31°45.5′ N.	159°57.2′ W.	Sept. 18	1905	1.03	100	412	33.1			
8	33°16′ N.	159°54′ W.	Sept. 19	1910	1.08	95	528	80.2	49.8	9 tunicates	32.8
10	34°51.5′ N.	159°51.4′ W.	Sept. 20	1905	1.05	100	67,476	113.4		68,600 barnacle larvae	75.2
12	36°30.5′ N.	159°51.3′ W.	Sept. 21	1904	1.02	90	17,307	59.9		16,500 barnacle larvae	24.8
16	41°06.4′ N.	159°58′ W.	Sept. 24	1919	1.10	100	12,137	158.5		9,300 barnacle larvae 3,600 euphausiids	94.4 11.1
20	46°13′ N.	159°57.5′ W.	Oct. 4	1906	1.03	95	8,678	82.1		5,300 barnacle larvae	1.7
25	36°33.2′ N.	174°47.5′ W.	Oct. 21	1910	1.00	100	170	65.4	15.1	8 tunicates	50.3
27	39°05′ N.	175°22′ W.	Oct. 24	1908	1.05	100	1,390	69.5			
Cruise 23:											
2	29°54.6′ N.	159°48′ W.	Dec. 6	1912	1.13	105	137	4.2			
6	34°39.5′ N.	160°01′ W.	Dec. 9	1913	1.20	100	1,533	55.6	16.0	44 tunicates	47.5
Cruise 24:			*1955*								
1	20°30.1′ N.	157°45.6′ W.	Mar. 24	1910	.93	100	238	24.3		5 tunicates	9.2
2	17°29.5′ N.	157°05′ W.	Mar. 25	2012	.97	90	202	88.6	30.0	1 fish	57.0
3	14°38′ N.	156°44′ W.	Mar. 26	2022	1.05	100	199	33.1			
4	11°58.9′ N.	156°13′ W.	Mar. 27	2017	1.00	90	283	42.5			
5	09°24′ N.	155°55.5′ W.	Mar. 28	2012	.97	90	877	114.2			
6	06°45′ N.	155°27′ W.	Mar. 29	2016	.97	95	853	92.3			
8	05°29′ N.	154°46.3′ W.	Mar. 30	2010	1.03	90	772	157.1	60.4	58 tunicates	99.6
10	03°48.6′ N.	154°49.8′ W.	Mar. 31	2005	1.00	95	605	311.3	28.3	38 tunicates	283.0
12	02°23.2′ N.	155°05.5′ W.	Apr. 1	2010	.97	100	560	64.0		18 tunicates	24.1
14	01°18.8′ N.	155°27.5′ W.	Apr. 2	2012	1.00	95	1,040	78.4			
18	02°37.2′ N.	157°43.8′ W.	Apr. 5	1920	.93	95	838	50.9			
20	03°11.9′ N.	158°39.3′ W.	Apr. 6	1916	1.00	90	557	156.4	33.6	20 tunicates	122.8
23	04°48.3′ N.	160°37.5′ W.	Apr. 8	1915	1.02	105	563	178.4	105.3	21 tunicates	74.6
Hugh M. Smith:											
Cruise 27:											
3	23°34.3′ N.	163°37.4′ W.	Jan. 7	1946	1.23	104	383	5.9			
5	22°39.2′ N.	166°56′ W.	Jan. 8	1946	1.12	112	678	10.8			
13	23°43.1′ N.	173°34.5′ E.	Jan. 14	2028	1.12	110	486	23.7			
15	24°45.1′ N.	170°41.1′ E.	Jan. 15	1940	1.02	110	482	12.6			
18	27°02′ N.	169°44.3′ E.	Jan. 16	1908	1.00	105	404	13.3			
21	29°46.7′ N.	169°48.2′ E.	Jan. 17	1917	1.00	105	1,020	48.9			
23–1	28°27.8′ N.	178°10.5′ W.	Jan. 31	1948	1.02	122	265	6.7			
25–2	30°02.5′ N.	179°31′ E.	Feb. 1	2049	1.02	122	1,487	28.1			
28–2	32°52′ N.	179°55.3′ W.	Feb. 2	2049	1.00	144	542	56.1			
32	36°57.5′ N.	175°03′ W.	Feb. 5	2048	1.03	135	1,157	31.6			
35	35°15.9′ N.	173°26.8′ W.	Feb. 6	2014	1.00	122	2,268	44.8			
37	32°34′ N.	173°01.5′ W.	Feb. 7	1911	.98	144	2,759	25.5			
40	29°36.1′ N.	172°42.5′ W.	Feb. 8	1911	.98	100	3,639	136.8	33.8	4 tunicates	101.0
43	26°31′ N.	172°02.5′ W.	Feb. 9	2055	1.00	122	302	101.9	6.9	1 tunicate	95.0
47	29°32′ N.	166°41.5′ W.	Feb. 12	1957	1.00	135	1,128	11.4			
49	32°28.1′ N.	166°44.3′ W.	Feb. 13	1901	1.00	100	2,350	69.8			
53	35°31.5′ N.	166°44′ W.	Feb. 14	1947	1.03	100	5,869	90.8			
55	37°07′ N.	164°17′ W.	Feb. 15	1932	1.00	104	2,698	88.0			
58	36°58.5′ N.	160°12.5′ W.	Feb. 16	1904	1.00	100	2,187	37.9			
62	33°56.2′ N.	159°42.8′ W.	Feb. 17	1912	1.02	100	4,732	68.9			
65	30°36′ N.	159°19.5′ W.	Feb. 18	1930	.98	100	1,890	37.8			
68	27°26.2′ N.	158°55.5′ W.	Feb. 19	1931	.98	100	731	13.5			
71	24°29.5′ N.	158°35.2′ W.	Feb. 20	1930	1.00	117	738	4.1			

[1] Total catch per hour less unusually large organisms or "jellies" constituting 50 percent or more of the catch.

APPENDIX TABLE 4.—*Summary of collection of organisms with 10-foot Isaacs-Kidd trawl, Hugh M. Smith cruises, central Pacific, 1955 and 1956*

Station	Position		Date	Start of haul	Length of haul	Estimated maximum depth	Catch/hour haul			Unusually numerous or bulky organisms	
	Latitude	Longitude					Number	Volume	Adjusted volume [1]	Number	Volume
			1955	*Zone time*	*Hours*	*Meters*		*Milliliters*	*Milliliters*		*Milliliters*
Cruise 27:											
23–2	28°32.1′ N.	178°10′ W.	Jan. 31	2102	1.00	118	882	57.1			
25–1	29°56.3′ N.	179°28.5′ E.	Feb. 1	1939	1.03	118	3,629	62.1			
28–1	32°46.5′ N.	179°54.5′ W.	Feb. 2	1943	.98	118	1,456	177.7			
Cruise 30:											
3	23°39′ N.	161°20′ W.	July 16	2005	2.17	192	560	97.0			
6	25°02′ N.	164°23′ W.	July 17	2038	.97	215	203	96.8	37.0	5 tunicates	58.0
9	26°11′ N.	167°17′ W.	July 18	2135	1.28	205	485	86.2			
12	27°11′ N.	170°54′ W.	July 19	1936	1.15	250	540	53.1			
15	27°47′ N.	174°00′ W.	July 20	2041	1.40	228	464	97.2			
18	27°37′ N.	177°58′ W.	July 23	2125	1.25	238	262	56.2			
21	30°17′ N.	179°53′ E.	July 24	2135	1.08	223	288	107.7			
23	33°41′ N.	180°00′	July 25	2130	1.20	275	237	131.2			
27	39°31′ N.	179°54′ W.	July 27	2123	1.15	224	1,116	180.3			
30	42°21′ N.	179°52′ W.	July 28	2139	1.55	253	1,215	211.0			
33	45°22′ N.	179°50′ W.	July 29	2134	1.00	204	1,539	188.0			
36	48°20′ N.	179°47′ W.	July 30	2149	1.23	200	6,865	347.6		9,450 euphausiids	207.0
38	49°30′ N.	177°19′ W.	July 31	2134	1.05	213	2,695	232.4		3 squids	79.0
40	49°25′ N.	172°35′ W.	Aug. 1	2131	.83	185	380	91.2			
42	46°57′ N.	172°31′ W.	Aug. 2	2132	.97	236	1,222	116.4			
45	44°37′ N.	172°27′ W.	Aug. 3	2236	.73	217	7,984	210.5			
48	41°08′ N.	172°22′ W.	Aug. 4	2200	.75	231	1,728	584.1	288.1	6 heteropods 59 pteropods	222.0 86.0
51	38°17′ N.	172°30′ W.	Aug. 5	2100	.98	231	1,047	150.0			
54	34°53′ N.	172°36′ W.	Aug. 6	2105	.57	206	793	64.6			
57	31°31′ N.	172°25′ W.	Aug. 7	2209	.68	206	676	77.2			
60	30°08′ N.	171°48′ W.	Aug. 8	2204	1.10	215	293	48.2			
63	29°54′ N.	168°32′ W.	Aug. 9	2101	1.00	210	259	133.1	77.1	5 tunicates	56.0
65	29°59′ N.	164°49′ W.	Aug. 10	2048	1.00	206	245	71.6			
67	32°49′ N.	164°59′ W.	Aug. 11	2049	.93	206	662	116.1	62.4	8 tunicates	50.0
69	36°00′ N.	164°53′ W.	Aug. 12	2104	.98	217	760	88.3			
75	42°22′ N.	164°55′ W.	Aug. 14	2101	1.10	218	1,335	431.3	223.1	103 heteropods	229.0
78	45°23′ N.	164°59′ W.	Aug. 15	2105	1.00	210	2,782	126.1			
80	48°01′ N.	164°55′ W.	Aug. 16	2104	1.20	206	934	186.3			
82	49°37′ N.	162°58′ W.	Aug. 17	2105	1.10	212	4,342	228.6			
85	49°34′ N.	157°55′ W.	Aug. 18	2100	1.07	211	252	99.0			
88	47°09′ N.	157°14′ W.	Aug. 19	2202	1.07	209	1,136	163.8			
95	41°23′ N.	157°24′ W.	Aug. 21	2134	1.03	214	212	245.3			
98	38°07′ N.	157°30′ W.	Aug. 22	2037	1.02	211	206	145.0	33.2	2 tunicates	114.0
101	34°54′ N.	157°30′ W.	Aug. 23	2030	1.25	206	252	62.2			
107	28°53′ N.	157°30′ W.	Aug. 25	2031	1.15	219	83	107.1			
110	25°53′ N.	157°30′ W.	Aug. 26	2005	1.02	211	213	75.0			
113	22°48′ N.	157°32′ W.	Aug. 27	2006	1.15	224	178	36.6			
Cruise 31:											
2	10°50′ N.	156°07′ W.	Sept. 26	2038	1.07	337	430	95.2			
5	07°55′ N.	155°18′ W.	Sept. 27	2045	1.75	339	285	39.0			
8	05°30′ N.	154°52′ W.	Sept. 28	2023	1.28	462	324	93.3			
11	06°25′ N.	153°24′ W.	Sept. 29	2030	1.92	382	461	166.7	78.0	Tunicates	108.2
14	08°21′ N.	150°59′ W.	Sept. 30	2024	1.05	337	378	159.4	58.5	7 tunicates	106.0
17	10°21′ N.	148°47′ W.	Oct. 1	2025	1.32	395	200	167.7	117.7	5 tunicates	66.0
20	11°00′ N.	147°15′ W.	Oct. 2	2027	1.08	433	326	74.1			
23	09°45′ N.	145°01′ W.	Oct. 3	2020	1.05	357	213	149.9	88.3	4 tunicates	64.7
26	08°37′ N.	142°41′ W.	Oct. 4	2023	1.17	298	261	156.8			
29	08°50′ N.	140°08′ W.	Oct. 5	2020	1.00	265	233	140.4			
32	10°25′ N.	137°48′ W.	Oct. 6	2022	1.08	337	365	157.2			
35	10°50′ N.	135°39′ W.	Oct. 7	2017	1.02	629	495	105.0			
38	09°40′ N.	132°58′ W.	Oct. 8	2015	.95	357	368	123.5			
41	09°30′ N.	130°01′ W.	Oct. 9	2026	1.03	337	296	777.0	75.0	Tunicates	723.0
44	10°30′ N.	127°20′ W.	Oct. 10	2023	1.03	379	437	1,510.5	73.7	1 fish; tunicates	800.0 680.0
47	11°33′ N.	125°06′ W.	Oct. 11	2012	1.00	298	596	2,206.8	206.8	1 fish	2,000.0
50	11°23′ N.	122°32′ W.	Oct. 12	2008	1.00	337	802	258.0	77.5	66 tunicates	180.5
53	09°30′ N.	120°03′ W.	Oct. 13	2010	.98	318	410	289.5	97.6	64 tunicates	188.1
56	09°10′ N.	117°35′ W.	Oct. 14	2012	1.00	337	313	209.8	122.8	30 tunicates	87.0
59	10°38′ N.	114°39′ W.	Oct. 15	2016	1.02	298	515	138.9			
62	12°20′ N.	112°30′ W.	Oct. 16	2011	1.02	322	317	208.3	43.6	31 tunicates	168.0
64	07°06′ N.	108°36′ W.	Oct. 27	2025	1.05	337	491	130.7			
67	04°39′ N.	109°24′ W.	Oct. 28	2002	1.00	318	631	106.7			
70	02°10′ N.	110°53′ W.	Oct. 29	1938	1.02	337	355	139.5			
73	00°12′ S.	112°25′ W.	Oct. 30	2003	1.02	375	334	132.5			
76	02°54′ S.	113°08′ W.	Oct. 31	2006	1.02	318	521	343.0	88.2	1 fish	260
79	05°24′ S.	113°18′ W.	Nov. 1	2019	1.02	413	931	93.6			
82	07°37′ S.	114°48′ W.	Nov. 2	2003	1.03	357	348	195.4	59.5	1 fish	140
86	06°43′ S.	120°06′ W.	Nov. 4	2015	1.03	329	436	63.2			
89	04°13′ S.	120°06′ W.	Nov. 5	2003	1.00	337	643	118.3			
92	01°32′ S.	120°05′ W.	Nov. 6	2017	1.02	318	1,289	203.6			
95	01°06′ N.	120°00′ W.	Nov. 7	2016	1.03	318	296	167.6			
105	03°54′ N.	120°01′ W.	Nov. 9	0005	1.02	375	304	946.9	220.7	Tunicates	740.7
109	05°52′ N.	119°53′ W.	Nov. 9	1955	1.03	357	483	191.3			
112	04°10′ N.	122°33′ W.	Nov. 10	2002	1.00	298	390	381.3	156.3	8 tunicates	225.0
115	02°03′ N.	125°05′ W.	Nov. 11	2011	1.05	318	1,178	297.6	195.6	129 tunicates	107.1
118	00°23′ N.	127°14′ W.	Nov. 12	2012	1.00	395	722	344.5	144.5	1 fish	200.0
121	01°28′ S.	129°24′ W.	Nov. 13	2008	1.00	357	5,818	474.7		5,124 euphausiids	355.0
124	01°09′ S.	131°48′ W.	Nov. 14	2005	1.02	375	497	144.0			
127	00°51′ N.	134°26′ W.	Nov. 15	2005	1.02	337	758	115.3			
130	03°00′ N.	136°56′ W.	Nov. 16	2010	.95	279	412	110.3			
133	05°40′ N.	139°15′ W.	Nov. 17	2107	1.00	375	482	241.0			

See footnote at end of table.

APPENDIX TABLE 4.—*Summary of collection of organisms with 10-foot Isaacs-Kidd trawl, Hugh M. Smith cruises, central Pacific, 1955 and 1956*—Continued

Station	Position		Date	Start of haul	Length of haul	Estimated maximum depth	Catch/hour haul			Unusually numerous or bulky organisms	
	Latitude	Longitude					Number	Volume	Adjusted volume [1]	Number	Volume
			1955	*Zone time*	*Hours*	*Meters*		*Milliliters*	*Milliliters*		*Milliliters*
Cruise 31—Con.											
136	03°31′ N.	139°15′ W.	Nov. 18	2005	1.02	357	378	181.5			
141	01°18′ N.	139°31′ W.	Nov. 19	2012	.95	379	480	164.4			
146	00°57′ S.	140°00′ W.	Nov. 20	2010	.95	318	158	348.2	132.8	Tunicates	204.6
151	04°03′ S.	139°49′ W.	Nov. 21	1955	1.02	318	314	136.1			
154	06°33′ S.	139°30′ W.	Nov. 22	2005	1.00	337	215	82.2			
164	06°37′ S.	141°53′ W.	Dec. 1	2010	1.02	337	319	134.0			
167	04°20′ S.	143°55′ W.	Dec. 2	2010	.90	279	988	122.1			
170	01°41′ S.	145°53′ W.	Dec. 3	2013	1.02	337	545	855.0	76.9	{Tunicates 1 heteropod	493.7 309.0
173	00°28′ N.	147°46′ W.	Dec. 4	2011	.93	239	566	753.8	311.1	Tunicates	411.7
176	01°07′ N.	149°56′ W.	Dec. 5	2010	.95	318	452	638.9	398.1	32 tunicates	228.8
179	00°09′ S.	153°00′ W.	Dec. 6	2013	.92	394	329	249.4	127.7	51 tunicates	1,120.0
Cruise 32:			*1956*								
3	21°01′ N.	157°54′ W.	Feb. 2	2105	.95	230	284	90.4			
11	21°20′ N.	158°21′ W.	Feb. 3	2025	1.00	189	432	35.7			
19	21°29′ N.	158°26′ W.	Feb. 4	1912	1.02	189	422	75.4			
31	22°02′ N.	157°44′ W.	Feb. 5	2025	1.00	192	628	66.7			
42	21°24′ N.	157°31′ W.	Feb. 6	2225	1.00	171	450	118.9			
47	21°15′ N.	158°38′W.	Feb. 8	1935	1.03	191	214	209.4	58.0	1 fish	156.0
49	21°19′ N.	158°33′ W.	Feb. 9	1920	1.02	221	152	34.3			
51	21°23′ N.	158°28′ W.	Feb. 10	1915	1.05	248	188	61.3			
Cruise 33:											
18	00°12′ N.	139°53′ W.	Mar. 18	2119	1.07	171	2,520	287.6			
20	00°01′ N.	139°27′ W.	Mar. 19	2104	.98	180	2,171	190.1			
21	01°07′ N.	140°07′ W.	Mar. 20	2105	1.02	171	3,476	173.0			
24	01°06′ N.	140°10′ W.	Mar. 22	2106	1.10	180	1,431	61.3			
28	01°14′ N.	140°35′ W.	Mar. 24	2114	.98	176	1,561	96.9			
Cruise 34:											
T1	21°38.5′ N.	158°25.7′ W.	May 7	1915	1.00	183	68	92.0			
T2	22°00.3′ N.	157°42′ W.	May 8	2000	1.00	176	318	49.0			
T3	21°16.7′ N.	157°31.5′ W.	May 9	1920	1.00	171	78	47.1			
T4	21°14.3′ N.	158°11′ W.	May 10	2120	1.00	166	413	114.6			
Cruise 35:											
1	21°21.5′ N.	158°15′ W.	Aug. 1	1930	1.10	176	192	158.7			
10	21°28.7′ N.	158°31.5′ W.	Aug. 2	2007	1.13	162	449	181.2			
20	22°15.7′ N.	157°56.4′ W.	Aug. 3	2020	1.17	180	262	92.0			
30	21°13.3′ N.	157°47.4′ W.	Aug. 4	1939	1.10	176	86	93.0	22.4	18 tunicates	77.7
54	09°33.2′ N.	134°52.4′ W.	Aug. 15	2014	1.00	180	482	195.0			
56	06°17′ N.	134°39.8′ W.	Aug. 16	2100	.95	191	699	210.0	107.9	32 tunicates	97.0
59	04°06.1′ N.	135°07.5′ W.	Aug. 17	2012	1.03	173	513	224.8	115.6	6 tunicates	112.5
61	01°30.5′ N.	135°13.6′ W.	Aug. 18	2005	1.03	176	887	164.4			
63	01°03.8′ S.	134°56′ W.	Aug. 19	2007	1.00	173	453	219.7	109.7	1 fish	110.0
66	04°33.6′ S.	134°58.5′ W.	Aug. 20	2007	1.08	176	313	145.5			
70	07°52′ S.	135°03.6 ′W.	Aug. 21	2006	1.02	176	156	161.5			
74	10°44.9′ S.	135°08′ W.	Aug. 22	2000	1.00	181	518	83.0			
78	14°14′ S.	135°01.9′ W.	Aug. 23	2000	1.00	180	389	59.3			
82	17°35′ S.	134°57.5′ W.	Aug. 24	2100	.98	181	186	64.3			
84	19°03.2′ S.	136°38.1′ W.	Aug. 25	2006	.95	171	57	12.4			
88	19°01′ S.	140°02.1′ W.	Aug. 26	2004	1.00	176	173	34.2			
91	18°57′ S.	143°00.5′ W.	Aug. 27	1947	1.00	166	33	7.9			
95	15°44′ S.	142°59.8′ W.	Aug. 28	1902	1.00	171	515	94.2			
99	12°21.2′ S.	143°03.7′ W.	Aug. 29	1900	1.00	166	1,109	167.6			
103	09°22.4′ S.	143°01.8′ W.	Aug. 30	1909	1.00	171	1,100	440.5	219.9	1 fish	221.5
107	06°15.1′ S.	143°03.8′ W.	Aug. 31	1901	1.00	176	293	114.3			
111	03°06′ S.	143°05.9′ W.	Sept. 1	1913	.98	166	612	310.1	152.4	74 tunicates	154.5
113	00°01.9′ N.	143°02.3′ W.	Sept. 2	2015	1.00	176	935	212.4			
115	02°02.4′ N.	144°34.7′ W.	Sept. 3	1903	1.00	189	838	253.4			
118	01°58.6′ N.	148°42′ W.	Sept. 4	2007	1.00	180	879	258.0			
121	00°27.9′ N.	151°13.8′ W.	Sept. 5	1958	1.00	176	788	368.9			
124	02°03′ S.	150°59.5′ W.	Sept. 6	2000	1.00	171	1,245	370.9	162.9	{589 euphausiids 1 fish	96.0 112.0
126	05°29.7′ S.	151°11′ W.	Sept. 7	2012	1.00	180	313	59.9			
129	08°41.9′ S.	150°59′ W.	Sept. 8	2000	1.00	171	579	147.1			
132	11°37′ S.	150°59.5′ W.	Sept. 9	2001	1.00	171	1,633	219.1	52.8	1,500 euphausiids	166.3
136	14°59.2′ S.	150°49.8′ W.	Sept. 10	2008	1.07	170	176	46.0	21.2	12 tunicates	26.5
138	17°02.2′ S.	150°18.4′ W.	Sept. 18	2007	1.00	176	45	30.1	10.8	11 tunicates	19.3
140	14°37′ S.	152°56′ W.	Sept. 19	2005	1.00	176	100	34.6	12.8	19 tunicates	21.8
143	14°30′ S.	156°05.5′ W.	Sept. 20	2005	1.00	166	131	33.3			
146	14°30′ S.	159°34′ W.	Sept. 21	1905	1.00	171	68	20.6			
150	11°51.5′ S.	160°11.5′ W.	Sept. 22	1905	1.00	180	140	55.2			
154	08°57.5′ S.	159°55.3′ W.	Sept. 23	1907	1.00	166	187	159.8	59.8	1 fish	100.0
158	05°57′ S.	160°04′ W.	Sept. 24	1904	1.00	176	960	202.7			
162	02°52.9′ S.	159°52.6′ W.	Sept. 25	1906	.97	166	1,561	189.8	114.5	1 squid	73.0
165	00°01.7′ N.	159°50′ W.	Sept. 26	1905	1.00	176	1,885	584.1	339.1	1 fish	245.0
168	04°19′ N.	160°08′ W.	Sept. 29	1905	1.00	176	1,466	441.9	210.9	7 siphonophores	73.5
										34 tunicates	157.5
170	07°38.3′ N.	160°00′ W.	Sept. 30	1904	.97	166	596	159.3			
173	10°27.9′ N.	160°02.2′ W.	Oct. 1	1905	1.00	180	485	111.7			
Cruise 37:											
24	11°19.3′ N.	162°07.9′ E.	Dec. 2	2031	.95	238	511	61.1			
33	11°20.6′ N.	162°07.8′ E.	Dec. 6	1956	.95	286	241	42.5			
42	11°21.7′ N.	162°05′ E.	Dec. 9	2012	1.05	278	452	23.4			
43	11°18.3′ N.	162°06.4′ E.	Dec. 9	2113	1.00	290	393	86.7			

[1] Total catch per hour less unusually large organisms or "jellies" constituting 50 percent or more of the catch.

APPENDIX TABLE 5.—*Checklist of organisms captured in 16 hauls with the 6-foot beam trawl, by areas, 1951–52*

Organisms	Size range (mm.)	Hawaiian waters		Equatorial Pacific		Total	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
COELENTERATA:							
Hydrozoa:							
Siphonophora	5-41	40	35	84	257	56	193
Scyphozoa:							
Coronatae:							
Periphyllidae:							
Periphylla sp.	70	10	1			6	1
Medusae: Unidentified	10-40	30	1	17	2	25	2
Other Coelenterata	<25	60	1	17	500	44	253
CHAETOGNATHA	9-44	100	29	100	178	100	90
ANNELIDA	157			17	1	6	1
ARTHROPODA:							
Crustacea:							
Copepoda	2-6	30	100	33	6	31	38
Mysidacea:							
Lophogastridae	20	10	10			6	10
Amphipoda:							
Hyperiidae	26-68			17	2	6	2
Phronimidae:							
Phronima sp.	20-32			67	9	25	9
Oxycephalidae:							
Oxycephalus sp.	20-33			67	13	25	13
Rhabdosoma sp.	28-75	10	1	67	36	31	29
Unidentified Amphipoda	<20			50	34	19	34
Stomatopoda (larvae)	7-53	90	36			56	36
Euphausiacea:							
Euphausiidae:							
Thysanopoda tricuspidata	20-27			33	28	12	28
Stylocheiron abbreviatum	22			17	1	6	1
Unidentified Euphausiacea	5-47	50	28	84	5,492	62	3,064
Decapoda:							
Sergestidae: Unidentified	20-70	40	6	50	76	44	36
Sergestes gardineri	20-31	20	5	17	24	19	11
Sergestes sp.	20-37	10	22	17	40	12	31
Lucifer sp.	<20			17	2	6	2
Penaeidae:							
Gennadas scutatus	22-40			33	2	12	2
Gennadas sp.	20-53	30	5	17	5	25	5
Funchalia taaningi	21-60			17	4	6	4
Hoplophoridae:							
Haplophorus typus	40-50	10	1	17	1	12	1
H. gracilirostris	48-65	20	2			12	2
H. grimaldii	27	10	1			6	1
Acanthephyra trispinosa	60-83	10	1	17	10	12	6
A. curtirostris	75	10	1			6	1
Acanthephyra sp.	62-78			17	6	6	6
Notostomus sp.	23	10	1			6	1
Systellaspis debilis	50-70	10	2			6	2
Pandalidae:							
Parapandalus zur strasseni	30-55	20	2	67	12	38	9
Parapandalus sp.	37-46			17	2	6	2
Scyllaridae: Phyllosoma	26	10	1			6	1
Unidentified Decapoda	10-40	10	12	67	152	31	124
Unidentified Crustacea	<20	60	(1)			38	(1)
Insecta:							
Hemiptera:							
Gerridae:							
Halobates sp.	<20			17	1	6	1
MOLLUSCA:							
Gastropoda:							
Pteropoda:							
Cymbuliidae	20-32			33	22	12	22
Unidentified Pteropoda	<20	10	(1)	17	62	12	(1)
Heteropoda:							
Pterotracheidae	20-40	50	4	17	1	38	3
Cephalopoda:							
Decapoda (squids):							
Enoploteuthidae	32			17	1	6	1
Chiroteuthidae	245	10	1			6	1
Cranchiidae	7-35	10	2	50	1	25	1
Unidentified Decapoda	5-40	10	7	33	4	19	5
Unidentified Mollusca	<20	10	(1)	33	25	19	(1)
UNIDENTIFIABLE INVERTEBRATE MATERIAL	<20	80	(1)	67	75	75	(1)
CHORDATA—Tunicata:							
Thaliacea:							
Pyrosomida:							
Pyrosomatidae	3-76	10	18	100	26	44	25
Salpida:							
Salpidae	17-105	10	35	100	62	44	58
Unidentified Tunicata	<20	40	(1)	50	283	44	(1)

[1] Actual number not determined.

APPENDIX TABLE 5.—*Checklist of organisms captured in 16 hauls with the 6-foot beam trawl, by areas, 1951–52*—Continued

Organisms	Size range (mm.)	Hawaiian waters		Equatorial Pacific		Total	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
CHORDATA—Vertebrata:							
Pisces:							
Gonostomidae: Unidentified		10	7			6	7
Ganostoma sp.	60	10	1			6	1
Vinciguerria lucetia	20–38	10	1	84	246	38	205
Cyclothone canina	20–50	10	56			6	56
Diplophos taenia	43–51	30	2	33	2	31	2
Sternoptychidae: Unidentified	30–40	10	3			6	3
Sternoptyx diaphana	11–12	10	2			6	2
Stomiatidae: Unidentified	20			17	1	6	1
Thysanactis sp.	87		17	17	1	6	1
Eustomias sp.	58–85	10	1	17	1	12	1
Chauliodontidae:							
Chauliodus sp.	43	10	1			6	1
Astronesthidae:							
Astronesthes lucifer	54	10	1			6	1
Malacosteidae:							
Photostomias sp.	65	10	1			6	1
Idiacanthidae: Unidentified	24	10	1			6	1
Idiacanthus fasciola	63	10	1			6	1
Synodontidae	40	10	1			6	1
Evermannellidae:							
Evermannella atrata	33			17	1	6	1
Myctophidae: Unidentified	15–46	50	7	67	18	56	12
Hygophum reinhardti	20			17	1	6	1
Benthosema sp.	27–31	20	2			12	2
Diogenichthys atlanticus	21	10	1			6	1
Centrobranchus nigro-ocellatus	41	10	1			6	1
Myctophum brachygnothos	36–45	10	2	17	1	12	2
M. spinosum	84–100	10	1	17	4	12	2
M. evermanni	20–46	10	4	50	4	25	4
M. aurolaternatum	28–31			33	1	12	1
Notolychnus valdiviae	21–27	30	3			19	3
Diaphus sp.	20–48	40	3	67	6	50	4
Lampanyctus pyrsobolus	20–61	20	1	33	2	25	2
L. tenuiformis	52			17	1	6	1
Lampanyctus sp.	20–70	40	10	50	7	44	9
Ceratoscopelus townsendi	20–58	20	4	67	9	38	7
Nemichthyidae:							
Serrivomer beani	133–230	10	1	17	1	12	1
Exocoetidae:							
Exocoetus volitans	142			17	1	6	1
Bregmacerotidae:							
Bregmaceros macclellandi	16–20			33	1	2	1
Melamphaidae:							
Melamphaes sp.	60–70			17	2	6	2
Apogonidae	20	10	1			6	1
Acanthuridae	21	10	1			6	1
Thunnidae:							
Kotsuwonus pelamis	18			17	1	6	1
Larval fish:							
Leptocephali: Unidentified	25–280	50	2	50	2	50	2
Heterosomata	17–28	40	2			25	2
Unidentified larvae	4–19	100	17	33	14	75	17
Unidentified Pisces	20–70	20	1	84	8	44	6

APPENDIX TABLE 6.—*Checklist of organisms captured in 23 hauls with the 1-meter ring trawl, by time of haul, central Pacific, 1953*

Organisms	Size range (mm.)	Percent occurrence	Average number per haul	Day hauls (11)		Night hauls (12)	
				Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
COELENTERATA:							
Hydrozoa							
Siphonophora	5–18	87	19	100	22	75	16
Medusae: Unidentified	20–70	13	1	9	1	17	1
CHAETOGNATHA	15–40	91	7	91	7	83	6
ANNELIDA	6	4	1	----	----	8	1
ARTHROPODA:							
Crustacea:							
Copepoda	3–5	48	27	36	26	58	27
Mysidacea:							
Lophogastridae:							
Gnathaphausia ingens	57	4	1	----	----	8	1
Amphipoda:							
Phronimidae:							
Phronima sp.	22–25	9	1	18	1	----	----
Oxycephalidae:							
Oxycephalus sp.	27–20	13	1	18	1	8	1
Rhabdosoma sp.	30–35	9	1	18	1	----	----
Unidentified Amphipoda	5–18	30	4	45	4	17	6
Stomatopoda (larvae)	11–43	43	2	45	2	42	2
Euphausiacea:							
Euphausiidae: Unidentified	5–33	83	33	82	20	92	39
Nematoscelis sp.	22	4	1	----	----	8	1
Stylocheiron sp.	24	4	1	----	----	8	1
Decapoda:							
Sergestidae: Unidentified	24–39	26	3	----	----	50	3
Sergestes gardineri	33	4	1	----	----	8	1
Penaeidae: Unidentified	22	9	1	9	1	8	1
Gennadas sp.	23–32	9	6	----	----	17	6
Hoplophoridae:							
Acanthephyra trispinosa	59	4	1	----	----	8	1
Pandalidae:							
Parapandalus zur strasseni	34–61	17	2	----	----	33	2
Palinuridae: Phyllosoma	16–30	9	1	9	1	8	1
Crab larvae: Unidentified	<20	13	3	----	----	25	3
Unidentified Decapoda	20–30	13	2	27	3	8	1
Unidentified Crustacea	<20	4	(1)	9	(1)	----	----
MOLLUSCA:							
Gastropoda:							
Pteropoda:							
Cavoliniidae:							
Cavolinia sp.	<20	4	1	9	1	----	----
Cymbuliidae	20	4	1	9	1	----	----
Unidentified Pteropoda	5–20	9	5	9	8	8	2
Heteropoda:							
Pterotracheidae	25–50	17	2	18	1	17	2
Cephalopoda:							
Decapoda (squids):							
Cranchiidae: Unidentified	11–15	9	1	9	1	8	1
Liocranchia globulus	9	4	1	----	----	8	1
Unidentified Decapoda	10–14	26	1	36	1	17	2
Larval Cephalopoda	13–18	9	(1)	9	(1)	8	1
UNIDENTIFIABLE INVERTEBRATE MATERIAL	<20	52	(1)	55	(1)	58	(1)
CHORDATA—Tunicata:							
Thaliacea:							
Pyrosomida:							
Pyrosomatidae	15–97	30	2	9	1	50	2
Salpida:							
Salpidae	20–82	52	2	27	4	67	2
Unidentified Tunicata	12–61	35	4	36	4	42	5
CHORDATA—Vertebrata:							
Pisces:							
Gonostomidae: Unidentified	35	4	1	----	----	8	1
Vinciguerria lucetia	20–23	4	2	----	----	8	2
Stomiatidae: Unidentified	20	4	1	----	----	8	1
Echiostoma tanneri	50	4	1	----	----	8	1
Idiacanthidae	35	4	1	9	1	----	----
Paralepididae	32	4	1	----	----	8	1
Myctophidae: Unidentified	>20	9	2	----	----	17	2
Notolychnus valdiviae	22–24	9	2	----	----	17	2
Diaphus sp.	20	4	1	----	----	8	1
Lampanyctus sp.	22–45	13	3	----	----	25	3
Ceratoscopelus townsendi	22–32	4	3	----	----	8	3
Nemichthyidae:							
Nemichthys scolopaceus	595	4	1	----	----	8	1
Exocoetidae	20	4	1	9	1	----	----
Bregmaceerotidae:							
Bregmaceros macclellandi	31	4	1	----	----	8	1
Aulostomidae:							
Aulostomus valentini	113	4	1	9	1	----	----
Bramidae:							
Collybus drachme	72	4	1	----	----	8	1
Thunnidae:							
Katsuwonus pelamis (juvenile)	18	4	1	----	----	8	1
Nomeidae	42	4	1	9	1	----	----
Larval fish:							
Leptocephali: Unidentified	20–80	13	1	9	1	17	2
Unidentified larvae	4–19	87	6	91	4	83	7
Unidentified Pisces	20–40	22	2	9	2	33	2

[1] Actual number not determined.

APPENDIX TABLE 7.—*Checklist of organisms captured in 78 hauls with the 6-foot Isaacs-Kidd trawl, by zones, 1953–55*

[For explanation of abbreviations of faunal zones, see p. 286]

Organisms	Size range (mm.)	SEC		ECC		NEC		Hawaii		NPC		AC		All zones	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
COELENTERATA:															
Hydrozoa:															
Siphonophora	5–65	100	77	100	46	100	37	74	35	100	149	80	257	92	102
Scyphozoa:															
Coronatae:															
Periphyllidae:															
Periphylla sp.	26			8	1									1	1
Medusae: Unidentified	20–80	11	7	50	2	66	1	5	1	50	2	5	1	26	2
Unidentified Coelenterata	29	6	1	8	2					5	2			4	2
CTENOPHORA	5–39	6	3	17	2			16	5	5	1			8	4
CHAETOGNATHA	6–50	100	94	83	78	100	17	95	38	88	64	50	41	87	62
Sagitta sp.				8	(1)									1	(1)
ANNELIDA	20–160							5	1	25	10	30	1	10	6
ARTHROPODA:															
Crustacea:															
Copepoda		6	(1)									20	500	4	(1)
Cirripedia:															
Lepadidae:															
Lepas fascicularis (larvae)	<20									6	68,640			1	68,640
Lepas sp. (larvae)	<20											40	8,025	5	2,006
Mysidacea:															
Lophogastridae: Unidentified	22	6	1					5	1					2	1
Lophogaster intermedius	20	6	1											1	1
Unidentified Mysidacea	<20	6	(1)											1	(1)
Amphipoda:															
Hyperiidae	76			8	1									1	1
Phronimidae:															
Phronima sp.	20–35	50	3	75	2			10	1	25	1	70	2	40	2
Oxycephalidae: Unidentified	22–60									19	2			4	2
Oxycephalus sp.	21–60	67	3	33	2	33	1			19	2	30	2	29	2
Rhabdosoma sp.	25–70	89	5	75	5			37	5	25	4	10	6	47	5
Unidentified Amphipoda	3–21	50	23	66	53	33	12	10	11			10	(1)	27	(1)
Stomatopoda (larvae)	10–48	11	1	17	1			47	8	19	2			20	5
Euphausiacea:															
Euphausiidae: Unidentified	5–35	100	355	83	240	100	74	47	114	69	1,225	80	2,375	76	681
Euphausia gibboides	20–25									19	16	20	5	9	10
Euphausia sp.	21–25											10	3	1	3
Thysanopoda monacantha	23–33							16	1	25	4			9	3
T. tricuspidata	20–26			8	82			5	1	12	1			6	17
Thysanopoda sp.	<20–30									12	4			2	4
Nematoscelis difficilis	20–23											10	1	1	1
Nematoscelis sp.				8	1									1	1
Nematobranchion flexipes	21–26									6	2	30	2	5	2
Stylocheiron maximum	21–28			8	4									1	4
Stylocheiron sp.	21–22			17	1									2	1
Decapoda:															
Sergestidae: Unidentified	12–55	28	20	33	53	66	5	26	14	50	5	70	22	40	18
Sergestes orientalis	23–35	11	11											2	11
S. gardineri	21–34	33	3	8	1									9	3
Sergestes sp.	20–65	67	20	33	31	33	5	37	33					30	25
Penacidae: Unidentified	22–27									6	2			1	2
Gennadas scutatus	20–39	50	9	42	17	66	2	16	1	12	1			27	8
Gennadas sp.	20–27	6	1	8	8									2	4
Funchalia taoningi	20–75	55	8	17	1			5	1	25	2			22	5
Benthesicymus sp.	21							5	1	5	1			1	1
Hoplophoridae															
Hoplophorus typus	20–64	61	6	33	1					6	1			20	4
H. gracilirostris	20–53	11	3					10	1	6	1			6	2
H. grimaldii	22–63							5	1	44	1	50	5	17	2
H. foliaceus	21–45	50	10	8	3			10	1					15	8
Hoplophorus sp.	20–31	17	10									20	2	6	7
Acanthephyra trispinosa	48–70			17	6			10	1					5	4
A. quadrispinosa	64											10	1	1	1
Acanthephyra sp.	39–55											20	2	2	2
Pandalidae:															
Parapandalus zur strasseni	21–59	78	4	42	5			5	1					26	4
Heterocarpus ensifer	135							5	1					1	1
Scyllaridae: Phyllosoma	21–31									6	1			1	1
Palinuridae: Phyllosoma	20–40			8	1			26	1	19	1			12	1
Portunidae: Megalopa	<20	8	1											1	1
Unidentified Decapoda	7–19	61	23	50	18	33	8	16	17	6	(1)			28	(1)
Unidentified Crustacea	3–20			25	33	66	20	74	155	56	912	80	975	46	475
MOLLUSCA:															
Gastropoda:															
Pteropoda:															
Cymbuliidae: Unidentified	20–32	72	3	8	2			10	5					20	3
Corolla sp.	20–80									38	1	70	6	17	4
Unidentified Pteropoda	5–45	11	3	17	2			21	40	25	50	60	125	23	62
Heteropoda:															
Pterotracheidae	20–50	89	4	25	10	33	1	32	3					33	4
Carinariidae:															
Carinaria sp.	24–45											10	2	1	2
Unidentified Heteropoda	35									6	1			1	1

[1] Actual number not determined.

APPENDIX TABLE 7.—*Checklist of organisms captured in 78 hauls with the 6-foot Isaacs-Kidd trawl, by zones, 1953–55*—Continued

Organisms	Size range (mm.)	SEC		ECC		NEC		Hawaii		NPC		AC		All zones	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
MOLLUSCA—Continued															
Cephalopoda:															
Decapoda (squids):															
Enoploteuthidae: Unidentified	21–81	22	1							12	1	20	2	10	1
Pterygioteuthis sp.	20–28	17	1					10	1					6	1
Abraliopsis sp.	22–125			8	11			10	1	6	1	10	2	6	3
Abralia sp.	45	6	1											1	1
Onychoteuthidae:															
Onychoteuthis banksii	30			8	1									1	1
Histioteuthidae	25											10	1	1	1
Chiroteuthidae:															
Mastigoteuthis sp.	20–25							5	1	6	1			3	1
Cranchiidae: Unidentified	25–32	11	1	17	2									5	2
Liocranchia globulus	77	6	1											1	1
Liocranchia sp.	<20–55	6	1	8	2									3	2
Helicocranchia sp.	20–41	11	4	8	1					6	1			5	3
Megalocranchia sp.	70							5	1					1	1
Unidentified Decapoda	20–100			17	1	33	1	5	2	44	1	30	3	18	2
Octopoda: Unidentified	<20									6	11			1	11
Bolitaenidae:															
Eledonella sp.	30–60			8	2									1	2
Argonautidae:															
Argonauta bottgeri	33			8	1									1	1
Unidentified Mollusca	3–20	67	15	33	14	66	8	42	10	31	31	10	50	41	17
CHORDATA—Tunicata:															
Thaliacea:															
Pyrosomida:															
Pyrosomatidae	4–370	100	29	75	24	100	13	58	3	75	7	40	3	73	16
Salpida:															
Salpidae: Undentified	20–190	94	10	83	18	100	3	74	22	94	158	90	193	87	70
Iasis zonaria	20–45									12	20	30	6	6	12
Doliolidae	12–50	11	13											2	13
Unidentified Tunicata	3–21	67	29	58	24	66	9	42	14	19	38			41	23
UNIDENTIFIABLE INVERTEBRATE MATERIAL	3–40	55	(1)	42	x	33	15	32	90	25	100	30	250	37	(1)
CHORDATA—Vertebrata:															
Pisces:															
Squalidae:															
Isistius brasiliensis	165–215	11	1			33	1							4	1
Alepocephalidae	21									6	1			1	1
Argentinidae: Unidentified	20									6	1			1	1
Nansenia sp.	24									6	1			1	1
Bathylagidae: Unidentified	60											10	1	1	1
Bathylagus ochotensis	42–95											30	2	4	2
Gonostomidae: Unidentified	22–106	6	1	8	1					12	3	10	1	6	2
Gonostoma elongatum	21–77	22	1	25	2	66	2	16	1					15	1
Vinciguerria lucetia	20–47	94	13	58	8	100	2	10	3	12	3			40	10
V. poweriae	20–33									25	3			5	3
V. nimbaria	20–36							21	2	19	11			9	6
Vinciguerria sp.	21–33							5	1	12	2			4	2
Diplophos taenia	34–48	6	1	17	3			5	1					5	2
Sternoptychidae:															
Argyropelecus sladeni	25–49			17	6									2	6
Stomiatidae: Unidentified	20–131	33	1	25	2	33	1	10	1	38	1	30	2	27	1
Thysanactis dentex	52–112	17	2	17	1	66	1	16	1					13	1
Thysanactis sp.	164–167	11	1	8	2	33	2							5	2
Leptostomias sp.	71	6	1											1	1
Bathophilus sp.	74–79	11	1											2	1
Eustomias sp.	60–157	17	1	25	3	33	1	5	1	6	1			12	2
Melanostomias sp.	95											10	1	1	1
Echiostoma tanneri	106–267	22	1											5	1
Photonectes sp.	75–175			8	1			5	1					2	1
Haplostomias tentaculatus	69							5	1					1	1
Chauliodontidae:															
Chauliodus sloanei	135			8	1									1	1
Chauliodus sp.	25–103	17	2					5	1	19	2			9	2
Astronesthidae: Unidentified	91–105									6	1			1	1
Astronesthes lucifer	31	6	1											1	1
A. richardsoni	75									6	1			1	1
Astronesthes sp.	26–55	22	1											5	1
Malacosteidae:															
Photostomias sp.	33–108	33	2	17	2			5	1					12	2
Aristostomias sp.	80–110	6	1	25	1	33	1							6	1
Idiacanthidae:															
Idiacanthus fasciola	192–333							10	1					9	1
I. panamensis	222–283			8	2	33	1							2	2
Idiacanthus sp.	26–360			17	2			5	1	25	5	10	3	4	4
Scopelarchidae: Unidentified	20–33									19	2	10	1	5	2
Scopelarchus sp.	20–39							5	2					1	2
Evermannellidae:															
Evermannella atrata	22–57			25	1									4	1
Evermannella sp.	67			8	1									1	1
Paralepididae	20–109	72	4	25	5			16	2	38	4	40	1	36	3
Alepisauridae	56							5	1	5	1			1	1

[1] Actual number not determined.

APPENDIX TABLE 7.—*Checklist of organisms captured in 78 hauls with the 6-foot Isaacs-Kidd trawl, by zones, 1953–55*—Continued

Organisms	Size range (mm.)	SEC		ECC		NEC		Hawaii		NPC		AC		All zones	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
CHORDATA—Vertebrata—Continued															
Pisces—Continued															
Myctophidae: Unidentified	20–105	61	6	25	5			53	4	88	12	90	10	60	8
Hygophum reinhardti	22–45	61	1	17	2	33	1	5	1					19	1
H. macrochir	25–34	6	1			33	1	5	1					4	1
Hygophum sp	46–47			8	3									1	3
Diogenichthys atlanticus	21–23	17	2											4	2
Myctophum asperum	36–68	6	1	8	1									2	1
M. affine	20	6	1	8	1									2	1
M. evermanni	20–56	44	7	33	2			5	1					17	5
M. rufinum	26			8	1									1	1
M. lychnobium	21	6	1											1	1
Myctophum sp	20–33	11	1											2	1
Lampadena nitida	21			8	1									1	1
Lampadena sp	39–45									6	1			1	1
Notalychnus valdiviae	20–24	22	18	8	9			10	1					9	12
Diaphus nipponensis	25									6	1			1	1
D. ostenfeldi	50			8	1									1	1
D. rafinesquei	47			8	1									1	1
Diaphus sp	20–85	100	9	75	5	33	1	21	2					41	7
Lampanyctus pyrsobolus	20–47	61	3	8	2			10	3					18	3
L. omostigma	51–56			17	2									2	2
Lampanyctus sp	20–122	78	4	75	6	100	5	26	3					40	4
Ceratoscopelus townsendi	20–62	44	2	58	2	66	4	10	1					24	2
Nemichthyidae: Unidentified	250–560			8	1							10	1	2	1
Nemichthys scolopaceus	292–680	17	1	8	1			5	1	19	2			10	1
Serrivomer beani	144–281			8	2									1	2
Hemirhamphidae	28			8	1									1	1
Bregmacerotidae: Unidentified	18–51							5	2					1	2
Bregmaceros macclellandi	22–77	50	2	33	2			5	1					18	2
Bregmaceros sp	20									6	1			1	1
Syngnathidae:															
Hippocampus sp	22							5	1					1	1
Trachypteridae:															
Trachypterus sp	25–118	6	1	17	2									4	2
Melamphaidae: Unidentified	9–26			8	1					6	1			2	1
Melamphaes sp	24–77			25	4									4	4
Serranidae	30	6	1											1	1
Priacanthidae:															
Priacanthus hamrur	20–24							5	2					1	2
Apogonidae:															
Howella sp	27–66	6	1	8	1									2	1
Bramidae:															
Collybus drachme	26–62	11	1											2	1
Coryphaenidae	37									6	1			1	1
Chaetodontidae	27							5	1					1	1
Brotulidae	37							5	1					1	1
Acanthuridae:															
Acanthurus sp	28	6	1											1	1
Gempylidae	20–46	11	1	17	2	33	4	5	1					8	2
Scombridae: Unidentified	<20	1	1											1	1
Dicrotus sp	22									6	1			1	1
Tetragonuridae:															
Tetragonurus sp	34			8	1									1	1
Larval fish:															
Leptocephali: Unidentified	40–350	11	1	66	2			42	2	19	3	40	1	32	2
Unidentified larvae	4–61	100	178	75	27	33	2	84	30	88	148	40	88	79	102
Unidentified Pisces	10–86	28	2	50	2	66	45	21	14	38	21	10	3	30	13

APPENDIX TABLE 8.—*Checklist of organisms captured in 157 hauls with the 10-foot Isaacs-Kidd trawl, by zones, 1955–56*

[For explanation of faunal zones, see p. 286]

Organisms	Size range (mm.)	SEC		ECC		NEC		Hawaii		NPC		AC		All zones	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
COELENTERATA:															
Hydrozoa:															
Siphonophora	5–450	78	71	77	57	78	31	67	41	100	88	63	61	76	62
Scyphozoa:															
Coronatae:															
Periphyllidae:															
Periphylla sp.	20–65	6	1	22	2	7	1							6	1
Medusae: Unidentified	3–100	26	2	44	3	57	1	25	7	46	5	74	109	38	27
Unidentified Coelenterata	5–100	25	76	39	38	21	50			8	200	16	98	20	70
CTENOPHORA	<20–70	3	10	11	10	7	2	4	6	23	3	58	7	13	7
CHAETOGNATHA	3–61	68	15	50	22	78	4	75	10	100	7	95	257	74	51
ANNELIDA	4–148	3	1			7	1			15	3	21	10	6	5
ARTHROPODA:															
Crustacea:															
Ostracoda	20									15	21	21	24	4	23
Copepoda	3–12	1	500					1	150	31	52	63	720	11	528
Mysidacea:															
Lophogastridae:															
Lophogaster sp.	20							8	2					1	2
Gnathophausia calcarata	30–68	4	1			7	1							2	1
G. longispina	50							4	1					1	1
Unidentified Mysidacea	15–16	1	1					8	10					2	6
Isopoda	<20	1	1											1	1
Amphipoda:															
Gammaridae	26–31	1	3											1	3
Cystisomatidae:															
Cystisoma sp.	28–90	9	1	11	2							5	1	6	1
Phronimidae: Unidentified	34									8	1			1	1
Phronima sp.	20–39	45	2	39	2	71	2	17	1	23	2	32	1	39	2
Phrosinidae:															
Phrosina sp.	20	3	1											1	1
Oxycephalidae: Unidentified	20–40	1	3					8	1					2	2
Oxycephalus sp.	20–82	45	4	33	2	21	1	12	1	31	1	16	3	32	3
Rhabdosoma sp.	28–95	51	4	39	6	7	1	25	4	15	2	5	1	33	4
Unidentified Amphipoda	3–70	38	24	11	11	21	9	29	13	38	23	58	43	34	25
Stomatopoda (larvae):															
Squillidae: Unidentified	20–50	10	2	6	1			38	2	8	2			11	2
Squilla sp.	20–42	1	1					17	2					3	2
Pseudosquilla sp.	20–40	1	2					25	1					4	1
Lysiosquilla sp.	25–35	4	1					8	1					3	1
Odontodactylus hanseni	29							4	1					1	1
Euphansiacea:															
Euphausiidae: Unidentified	5–33	64	275	39	128	57	163	71	116	77	97	95	522	66	258
Euphausia pacifica	7–23											63	629	8	629
E. eximia	20–23	9	320	6	1	21	1							6	192
E. lamelligera	20									8	1	5	1	2	1
E. gibboides	20–30	12	8							15	4	10	4	8	7
Euphausia sp.	20–31	4	1									5	2	2	1
Thysanopoda monacantha	20–40	45	9	89	16	43	15	46	2	62	3	5	1	46	9
T. cristata	23–40	3	1	6	2			12	4	8	2			4	2
T. tricuspidata	20–33	68	91	39	15	14	1	12	1	8	1			38	73
T. aequalis	20–22							25	2					4	2
T. obtusifrons	20–24	1	2			28	2	25	6	46	4	5	8	11	4
T. pectinata	20–38	16	2	44	2	14	5	12	2					15	2
T. orientalis	21–37	6	2	11	2	14	2	8	2					6	2
T. acutifrons	23–40	3	1	6	3			4	1			37	6	7	4
Thysanopoda sp.	20–36	7	51			7	31	4	1	15	3	5	7	6	30
Tessarabrachion oculatus	20–32											37	7	4	7
Thysanoessa spinifera	21–26											16	8	2	8
T. longipes	20–26											26	25	3	25
Nematoscelis difficilis	20–23									8	1	10	24	2	16
N. atlantica	20							4	1					1	1
N. tenella	20–21			6	2									1	2
Nematoscelis sp.	20–24	6	2					17	1					5	2
Nematobrachion flexipes	20–27	9	1	6	2	36	3	20	1	15	2			12	2
N. sexspinosus	24–29					7	4	4	2					1	3
Nematobrachion sp.	20–24									8	3	5	30	1	16
Stylocheiron abbreviatum	20–37	6	1	50	2	7	1	4	2			47	9	15	4
S. maximum	20–25											5	6	1	6
Stylocheiron sp.	21–40									8	6	10	8	2	7
Decapoda:															
Sergestidae:															
Sergestes prehensilis	60									8	1			1	1
Sergestes sp.	20–100	94	45	94	31	93	20	96	19	92	4	95	42	94	34
Penaeidae: Unidentified	<20–33	3	20	11	70	7	35	8	1					4	31
Penaeus sp.	20							4	4					1	4
Gennadas scutatus	20–32	38	4	78	11	50	12							30	7
G. propinquus	20–45	29	3	44	3	28	2	12	4	31	3	16	3	27	3
G. tinayrei	20–30	7	1	28	1	14	2	12	2					10	1
G. incertus	20–45	22	4	33	3	21	2	12	1	46	3	26	3	24	3
G. bouvieri	20–32	7	2			28	3							6	2
G. parvus	20			6	1									1	1
Gennadus sp.	<20–45	42	6	56	14	57	9	54	4	8	1	5	1	39	7
Bentheogennema pasithea	32–42	3	1			21	1							3	1
Funchalia balboae	105							4	1					1	1
F. taaningi	20–80	33	3	17	3	7	1	4	1					18	3
Funchalia sp.	25–85	12	8	11	2			4	1	15	1			8	5

APPENDIX TABLE 8.—*Checklist of organisms captured in 157 hauls with the 10-foot Isaacs-Kidd trawl, by zones, 1955–56*—Continued

Organisms	Size range (mm.)	SEC		ECC		NEC		Hawaii		NPC		AC		All zones	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
ARTHROPODA—Continued															
Crustacea—Continued															
Decapoda—Continued															
Pasiphaeidae:															
Pasiphaea flagellata	80					7	7							1	7
Pasiphaea sp	20–63	1	1			21	1							2	1
Hoplophoridae: Unidentified	<20–68	7	32					17	1					6	18
Hoplaphorus typus	33–76	32	3	17	3									16	3
H. longirostris	50–63	4	1			7	2	4	1					3	1
H. gracilirostris	20–78	9	4			7	2	42	8					11	6
H. grimaldii	22–80	1	2					25	3	85	3	10	10	13	4
H. foliaceus	20–60	45	8	11	2	7	1	21	2	8	3			25	7
Hoplophorus sp	20–70	4	1			14	1	8	2					4	1
Acanthephyra trispinosa	20–103	33	3	72	6	43	3							27	4
A. sanguinea	70–80	1	3											1	3
A. stylorostrata	50	1	1											1	1
A. quadrispinosa	55–90	1	1							15	2	16	3	4	2
A. gracilipes	28							4	1					1	1
Acanthephyra sp	22–62	1	1	6	2	7	4	4	1	8	12	5	(1)	4	(1)
Notostomus sp	54–95											5	3	1	3
Systellaspis debilis	45–82					14	2	38	2					7	2
Systellaspis sp	60–73					7	5							1	5
Hymenodora sp	50											5	1	1	1
Thalassocaridae:															
Thalassocaris sp	20	6	3											2	3
Pandalidae: Unidentified	22–55	7	1	11	2	14	2							6	1
Parapandalus zur strasseni	27–60	40	6	39	8	7	2	25	1	15	2			28	5
P. cattei	47	1	1											1	1
Parapandalus sp	37–55							8	2	15	2	5	2	3	2
Plesionika sp	45–67	1	1	6	6									1	4
Heterocarpus sp	40							4	1					1	1
Portunidae	20							4	1					1	1
Phyllosoma	11–40	16	2	6	1			12	2	8	1			10	2
Unidentified Decapoda	19–72	7	16			7	3	12	4	38	25	32	31	13	20
Unidentified Crustacea	2–90	61	288	89	136	86	208	75	136	54	596	32	118	64	238
MOLLUSCA:															
Gastropoda:															
Pteropoda:															
Cymbuliidae	20–60			6	1			4	1	31	2	21	11	6	5
Unidentified Pteropoda	5–60	32	28	6	2			21	6	54	24	47	33	28	26
Heteropoda:															
Carinariidae:															
Carinaria sp	29–36					7	1			8	1			1	1
Atlantidae	<20	1	1											1	1
Unidentified Heteropoda	20–177	22	2	11	1	14	1	12	3	8	1	16	40	16	6
Cephalopoda:															
Decapoda (squids):															
Enoploteuthidae: Unidentified	20–285	17	1	6	2							5	1	9	1
Enoploteuthis sp	20–260	1	1	6	2			4	1			5	1	2	1
Abralia trigonura	59–100	3	2	6	1									2	2
A. astrosticta	33–50	3	2											1	2
Abralia sp	20–60	10	2											4	2
Abraliopsis morisii	40–70					7	2							1	2
Abraliopsis sp	20–100	12	2	28	7	7	2	4	1	8	1	21	2	13	3
Pterygioteuthis giardi	20–50	12	2			7	1							6	2
P. microlampas	30							4	1					1	1
Pterygioteuthis sp	20–35	4	1	11	2									3	1
Pyroteuthis margaritifera	50–100									15	1	5	2	2	1
Onychoteuthidae: Unidentified	35	1	1											1	1
Onychoteuthis banksii	310	1	1											1	1
Veranyidae:															
Octopodoteuthis sp		1	1											1	1
Histioteuthidae: Unidentified	25–110	7	1	6	1			12	1					6	1
Histioteuthis sp	35–132					7	1					5	1	1	1
Calliteuthis meleagroteuthis	115–150									15	1			1	1
Bathyteuthidae:															
Benthoteuthis sp	30–60	1	2	6	1									1	2
Ctenopteryx sp	20	1	1											1	1
Brachioteuthidae:															
Brachioteuthis sp	35									8	1			1	1
Ommastrephidae: Unidentified	230	1	1											1	1
Symplectoteuthis oualaniensis	47	1	1											1	1
Chiroteuthidae: Unidentified	60–100					7	1	4	1					1	1
Chiroteuthis imperator	20–510											16	2	2	2
Chiroteuthis sp	50	1	1											1	1
Mastigoteuthis sp	30							4	1					1	1
Doratopsis sp	20					7	1							1	1
Cranchiidae: Unidentified	20–180	10	1	6	1			8	1	15	1	10	2	9	1
Cranchia scabra	20–205	7	1	6	1									4	1
Liocranchia globulus	20–135	10	1	6	1									5	1
L. valdiviae	20–25	2	2	6	3									2	2
Liocranchia sp	20–210	7	1	6	2			4	1					4	1
Helicocranchia sp	34–35	1	1							8	1			1	1
Desmoteuthis sp	30–45	3	2											1	2
Corynomma sp	32			6	1									1	1
Euzygaena pacifica	40					7	1							1	1
Euzygaena sp	20–31			6	1	7	1							1	1

[1] Actual number not determined.

APPENDIX TABLE 8.—*Checklist of organisms captured in 157 hauls with the 10-foot Isaacs-Kidd trawl, by zones, 1955–56*—Continued

Organisms	Size range (mm.)	SEC		ECC		NEC		Hawaii		NPC		AC		All zones	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
MOLLUSCA—Continued															
Cephalopoda—Continued															
Decapoda—Continued															
Unidentified Decapoda	19–205	22	3	28	1	21	1	4	1			10	3	16	2
Octopoda: Unidentified	7–30	3	1	6	1					8	1	10	2	4	1
Unidentified Cephalopoda	3–85	1	2					12	10			26	3	6	5
Unidentified Mollusca	<20	10	28	17	12	7	5	21	19			5	3	11	20
CHORDATA—Tunicata:															
Thaliacea:															
Pyrosomida:															
Pyrosomatidae	20–310	65	26	72	5	71	12	83	6	92	6	21	4	66	15
Salpida:															
Salpidae: Unidentified	5–180	56	34	56	7	71	5	50	16	92	64	58	54	60	35
Salpa sp.	20–110	1	6	17	6									2	6
Ritteriella sp.	60					7	1							1	1
Metcalfina hexagona	20–150	3	1	22	7	28	4							6	5
Thetys vagina	35–220	1	3	33	5	21	6			8	1			7	5
Iasis zonaria	<20–66	17	9	33	9	36	3	4	1	8	14	5	2	16	7
Unidentified Tunicata	16–55	35	41	44	30	50	18	8	50			5	5	27	34
CHORDATA—Vertebrata:															
Pisces:															
Squalidae: Unidentified	380	1	1											1	1
Isistius brasiliensis	202–360	4	1											2	1
Alepocephalidae	34			6	1									1	1
Dolichopterygidae:															
Bathylychnops exilis	115											5	1	1	1
Argentinidae	23–59			6	1							5	4	1	2
Bathylagidae:															
Bathylagus nigrigenys	20–85	1	2	11	2	36	4							5	3
B. bericoides	107–122	2	1											1	1
B. longirostris	112–146							8	2	8	1			2	2
B. ochotensis	25–107											16	6	2	6
Bathylagus sp.	50–153	1	2	6	3	7	1			8	1	16	14	4	7
Gonostomidae: Unidentified	20–130	13	14	11	1			8	2	15	1			10	9
Gonostoma elongatum	35–195	25	4	6	1			33	3	31	2			19	3
G. denudatum	48					7	1							1	1
Gonostoma sp.	38–197	12	8	6	2	21	2					47	12	13	8
Cyclothone sp.	38	1	1											1	1
Margrethia sp.	110–115	1	2											1	2
Vinciguerria lucetia	20–54	3	8	56	5	43	25			8	1			12	11
V. poweriae	21							4	1					1	1
V. nimbaria	21–40	1	1					54	2	54	2	10	4	15	2
Vinciguerria sp.	20–62	54	8	28	13	14	2	33	4	15	4			34	8
Diplophos taenia	38–166	9	1	17	1			12	1					8	1
Ichthyococcus ovatus	42–75	1	1									10	1	2	1
Sternoptychidae: Unidentified	41			6	1									1	1
Sternoptyx diaphana	20–53	1	1	6	3					8	1	5	1	2	2
Argyropelecus oculeatus	31–72	12	2	50	5	43	6	8	2	38	2	5	2	20	4
A. sladeni	37–57	1	1	6	2					8	1	47	5	8	4
A. affinis	35–50					14	2							1	2
Argyropelecus sp.	20–45	7	2	17	8									5	4
Polyipnus sp.	37–55					7	1					5	1	1	1
Stomiatidae: Unidentified	22–195	43	4	33	2	14	1	33	2	46	2			33	3
Stomias nebulosus	63–106	1	8											1	8
Stomias sp.	22–195	20	4											9	4
Opostomias micripnus	165–215									8	2			1	2
Opostomias sp.	107–185									15	2			1	2
Thysanactis dentex	40–160	17	2	6	1	7	1	4	2					10	2
Thysanactis sp.	50–190	1	5											1	5
Leptostomias sp.	95–225	6	1											2	1
Bathophilus filifer	75–105	7	2	11	2	28	2							7	2
B. pawneei	63	1	1	6	1									1	1
B. metallicus	115	1	1											1	1
Bathophilus sp.	20–90	1	1	6	7	7	1			8	1			2	2
Eustomias brevifilis	65	1	1											1	1
E. enbarbatus	72–76	1	2											1	2
E. patulus	185	1	1											1	1
E. longibarba	75	1	1											1	1
E. schmidti	175			6	1									1	1
Eustomias sp.	50–205	38	2	11	1	21	1	21	1					23	2
Melanostomias albibarba	220	1	1											1	1
Melanostomias sp.	55–135	4	1											2	1
Echiostoma tanneri	33–280	7	3											3	3
Echiostoma sp.	100							4	1					1	1
Photonectes sp.	125–175			6	1	7	1	4	1			32	5	6	4
Chauliodontidae:															
Chauliodus barbatus	25–122	1	20											1	20
Chauliodus sp.	22–210	40	3	22	2			21	1	23	1	26	2	29	2
Astronesthidae: Unidentified	20–209	9	1	6	1			17	1	15	1	5	1	9	1
Astronesthes richardsoni	76									8	1			1	1
A. cyaneus	90–120	7	1	6	1									4	1
A. indicus	23–165	6	2	6	1									3	2
A. filifer	96	1	1											1	1
A. caulophorus	110			6	1									1	1
Astronesthes sp.	25–131	13	1					8	1					7	1
Heterophotus ophistoma	160–190	3	1											1	1

APPENDIX TABLE 8.—*Checklist of organisms captured in 157 hauls with the 10-foot Isaacs-Kidd trawl, by zones, 1955–56*—Continued

Organisms	Size range (mm.)	SEC		ECC		NEC		Hawaii		NPC		AC		All zones	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
CHORDATA—Vertebrata—Continued															
Pisces—Continued															
Malacosteidae: Unidentified	38-95	6	2	6	2									3	2
Photostomias sp.	50-102	13	2					8	1					7	2
Aristostomias scintillans	137	1	1											1	1
Aristostomias sp.	50-170	2	1					12	2					3	2
Idiacanthidae:															
Idiacanthus fasciola	75-345	1	3			7	2					16	1	4	2
I. panamensis	220-365					21	2							2	2
Idiacanthus sp.	22-330	20	2	17	1	36	2	50	1	8	1	5	1	23	2
Synodontidae	35							4	1					1	1
Aulopidae	72							4	1					1	1
Scopelarchidae: Unidentified	20-95	10	2			21	1	8	1	15	1	5	1	10	1
Scopelarchus analis	24-85	3	2			7	1	8	2			5	5	4	2
Scopelarchoides nicholsi	55			6	1									1	1
Evermannellidae: Unidentified	21-38	13	2	6	1									6	2
Evermannella atrata	36-110	7	1	6	1	14	1							5	1
E. indica	50-63	1	2	11	2									2	2
E. normalops	93	1	1											1	1
E. balbo	26-56	1	3											1	3
Evermannella sp.	32	1	1											1	1
Paralepididae: Unidentified	20-147	39	2	28	2	29	1			15	2	32	2	30	2
Lestidium japonicum	230	1	1											1	1
Lestidium sp.	260	1	1											1	1
Myctophidae: Unidentified	20-168	81	21	50	16	50	8	67	12	54	14	32	4	64	17
Electrona crockeri	35											5	1	1	1
E. rissoi	20-46											26	2	3	2
Electrona sp.	25-44											26	2	3	2
Hygophum reinhardti	35	1	1											1	1
H. hanseni	20-58	3	2							8	1			2	2
H. benoiti	20-40							4	6					1	6
Hygophum sp.	21-60	22	3	6	1	14	2	17	1	8	(1)	10	1	16	(1)
Benthosema suborbitale	23-35	1	2					21	5	15	4	5	3	6	4
B. fibulata	20	1	1											1	1
Benthosema sp.	22-23	3	2											1	2
Diogenichthys laternatus	22-30	4	2	17	9									4	6
D. atlanticus	21-24	3	1					4	1	23	1			4	1
D. panurgus	21-27					7	3							1	3
Diogenichthys sp.	22-29					14	2							1	2
Gonichthys cocco	31	1	1											1	1
G. tenuiculum	43			6	1									1	1
Centrobranchus nigro-ocellatus	33-43	1	1					4	4					1	2
Tarletonbeania sp.	38-64											10	4	1	4
Myctophum asperum	36-66	4	1											2	1
M. brachygnathos	29-72							8	2					1	2
M. aurolaternatum	35	1	1											1	1
M. spinosum	92	1	1											1	1
M. affine	21-55	3	1			7	1	4	1	8	1			3	1
M. evermanni	21-70	19	3	11	2			17	2					12	3
M. rufinum	63					7	1							1	1
M. californiense	30											5	1	1	1
Myctophum sp.	20-80	7	4	11	1			17	2			5	2	8	3
Ctenoscopelus phengodes	112	1	1											1	1
Lampadena nitida	72							4	1					1	1
Lampadena sp.	22-83	7	1					12	1					5	1
Notolychnus valdiviae	20-29	8	14					8	4	15	1			6	9
Diaphus theta	65							4	1					1	1
D. nipponensis	29-55							4	1					1	1
Diaphus sp.	20-105	48	12	22	8	36	5	42	6	54	15	58	5	44	10
Lampanyctus pyrsobolus	20-55	33	2	11	2			29	2					20	2
L. macropterus	23-103	22	6	6	5	7	3	4	4					11	6
L. festivus	32-75	1	6							8	2			1	4
L. microchir	24-35	1	5											1	5
L. omostigma	25-105	3	2	6	3									2	2
L. steinbecki	20-60	3	6					4	1	8	1			2	4
L. leucopsorus	20-113											37	12	4	12
L. nannochir	48											5	1	1	1
L. ritteri	45-110					7	6					5	6	1	6
L. regalis	44-80											10	4	1	4
L. tenuiformis	39	1	1											1	1
Lampanyctus sp.	20-135	32	5	28	7	64	2	33	6	31	3	63	4	38	4
Cerotoscopelus townsendi	22-100	46	7	11	1			38	3	31	2	10	3	31	5
C. maderensis	20-28					7	4							1	4
Notoscopelus sp.	57-67									8	1	5	1	1	1
Cetomimidae	85-100					7	1	4	1					1	1
Giganturidae:															
Giganturo indica	80					7	1							1	1
Nemichthyidae: Unidentified	35			6	1									1	1
Nemichthys scolopoceus	110–1,200	29	2	22	1	28	1	4	1	8	1	5	1	20	2
Avocettina infans	170-390	1	1	17	2	28	6					5	1	6	4
Serrivomer beani	40-320	1	1	39	2	28	1							8	2
Belonidae	35-65	1	2											1	2
Scomberesocidae	86			6	1									1	1
Hemirhamphidae	24-34	3	1											1	1

[1]Actual number not determined.

APPENDIX TABLE 8.—*Checklist of organisms captured in 157 hauls with the 10-foot Isaacs-Kidd trawl, by zones, 1955–56*—Continued

Organisms	Size range (mm.)	SEC		ECC		NEC		Hawaii		NPC		AC		All zones	
		Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul	Percent occurrence	Average number per haul
CHORDATA—Vertebrata—Continued															
Pisces—Continued															
Exocoetidae: Unidentified	20–28	1	1											1	1
Exocoetus sp.	53–65			6	1			4	1					1	1
Bregmacerotidae: Unidentified	20–51	1	1	6	1									1	1
Bregmaceros macclellandi	20–95	23	2	11	2			8	2					13	2
Bregmaceros sp.	38–50	3	1											1	1
Gadidae:															
Melanonus sp.	80–96	3	1											1	1
Fistularlidae	50	1	1											1	1
Trachypteridae: Unidentified	300–920			11	1									1	1
Trachypterus cristatus	413	1	1											1	1
Trachypterus sp.	82–555	6	1											2	1
Caulolepidae:															
Anoplogaster cornutus	76–80	1	2											1	2
Diretmidae:															
Diretmus argenteus	24–72	4	1	6	1									2	1
Holocentridae	21							4	1					1	1
Melamphaidae: Unidentified	20–70	20	1	56	3	43	5	4	1	15	2	16	2	23	2
Melamphaes suborbitalis	31–52			6	1	7	1					5	(1)	2	x
M. frontosus	24–90	1	2			7	1	4	1	8	2			2	2
M. robustus	38									8	1			1	1
M. beanii	20–50							8	2					1	2
M. mizolepis	49–50			6	2									1	2
Melomphaes sp.	22–77	1	2	6	4	14	3	4	1	8	1	10	1	5	2
Zeidae	55–65	1	2											1	2
Serranidae:															
Planctanthias sp.	21–33	1	1					4	7					2	4
Apogonidae:															
Howella sherborni	20–64	16	1	11	1	7	2	4	1					10	1
Howella sp.	40											5	1	1	1
Carangidae: Unidentified	20							4	1					1	1
Decapterus pinnulatus	78–90							4	3					1	3
Bramidae: Unidentified	25–36	3	1	6	1									2	1
Brama rai	42–65	3	2											1	2
Collybus drachme	30							4	1					1	1
Chaetodontidae	21–27							12	1					2	1
Chiasmodontidae: Unidentified	110–133	1	1	6	1	7	1							2	1
Pseudoscopelus cephalus	35	1	1											1	1
Pyramodontidae:															
Snyderidia sp.	210–220							4	3					1	3
Brotulidae: Unidentified	28–51	1	1					4	1					1	1
Brotula multibarbata	44							4	1					1	1
Gempylidae: Unidentified	20–175	16	3	6	1			17	1					10	2
Gempylus serpens	70–170	1	1	6	1	7	1	8	1					3	1
Trichiuridae: Unidentified	82							4	1					1	1
Benthodesmus sp.	80	1	1											1	1
Nomeidae: Unidentified	32	1	1					4	1					1	1
Cubiceps sp.	20							4	1					1	1
Psenes sp.	24	1	1											1	1
Thunnidae: Unidentified	20–60									8	2			1	2
Katsuwonus pelamis	22	1	1											1	1
Bothidae	41									8	1			1	1
Monacanthidae:															
Pervagor melanocephalus	30	1	1											1	1
Ostraciidae:															
Lactoria diophanus	70					7	1							1	1
Diodontidae	26							4	1					1	1
Molidae: Unidentified	<20	1	8					4	12					1	10
Mola mola	20	1	1											1	1
Ranzania laevis	25–42	2	2											1	2
Masturus sp.	20	1	1											1	1
Himantolophidae:															
Himantolophus groenlandicus	300					7	1							1	1
Ceratiidae:															
Cryptopsaras couseii	25									8	1			1	1
Leptocephali: Unidentified	42–350	52	2	17	8	7	1	25	1	46	2	10	2	34	2
Unidentified Pisces	3–130	88	29	89	19	93	14	88	21	85	49	68	16	86	26
UNIDENTIFIABLE MATERIAL	<20–48	14	45	6	75	14	62	58	46	23	100			19	53

[1] Actual number not determined.

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DISTRIBUTION OF TUNAS IN OCEANIC WATERS OF THE NORTHWESTERN ATLANTIC

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The increased importance attached to commercial utilization of tunas during the past decade has increased the importance of studies of the habits and life histories of the principal tuna species and investigations of areas known or thought to be inhabited by tunas.

Seasonal tuna fisheries have been carried out for many years on the Continental Shelf between Newfoundland and Cape Hatteras by commercial and sport fishermen. But the short season and fluctuating availability of the stocks—principally bluefin and little tuna—have made commercial operations economically hazardous. Since the early 1950's the U.S. Bureau of Commercial Fisheries has worked to reduce the fluctuations in availability through introduction and development of diverse types of commercial gear. This work has culminated recently near Cape Cod in a successful commercial purse seining venture (Squire, 1959), which, in 1959, landed 750 tons of bluefin tuna in 21 days of fishing—a record for the Cape Cod area.

In addition, the Bureau and the Woods Hole Oceanographic Institution have conducted research on the life history of bluefin in attempts to understand the resource more fully, but the life history studies have been seriously hampered by the almost complete lack of knowledge of bluefin during periods when they are absent from the inshore regions. Prior to 1957, knowledge of tunas in the oceanic region of the northwest Atlantic was practically nonexistent, in sharp contrast to the extensive body of knowledge concerning tunas of inshore and oceanic regions of the Pacific that had been gained through continuing research.

Note.—The author is presently Fishery Research Biologist, Tiburon Marine Laboratory, Bureau of Sport Fisheries and Wildlife, U.S. Fish and Wildlife Service, Tiburon, Calif.

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In 1957, the Bureau's North Atlantic Fisheries Exploration and Gear Research Base began an investigation of the broad oceanic region adjacent to the Continental Shelf of northeastern North America. Primary objectives were to determine the distribution patterns of the dominant tuna species inhabiting these oceanic waters and to determine the availability of tunas to commercial gear. Eight cruises of the Bureau research vessel *Delaware* were made during the investigation, which was conducted intermittently from March 1957 through May 1960. Explorations with longline gear were made during at least some portion of all seasons. Represented in the catches were tunas of six species—bluefin (*Thunnus thynnus*), yellowfin (*Thunnus albacares*), albacore (*Thunnus alalunga*), bigeye (*Thunnus obesus*), blackfin (*Thunnus atlanticus*), and skipjack (*Euthynnus pelamis*). The first three are dominant tuna species in the region explored.

This paper firstly reviews the status of tuna knowledge in the northwestern portion of the Atlantic at the start of the investigation; secondly, describes the exploratory methods and procedures used, the physical characteristics of the area explored, the seasonal and geographic distribution of dominant tuna species of the oceanic region, and the occurrence of other tuna species in the region; and thirdly, discusses the relation between the tunas of the oceanic region and those of the Continental Shelf.

The investigation was facilitated greatly by cooperation with Boston University and the Woods Hole Oceanographic Institution. In particular, acknowledgment is made of the efforts of Robert H. Gibbs, Jr., Boston University, and Frank J. Mather III, Woods Hole Oceanographic Institution.

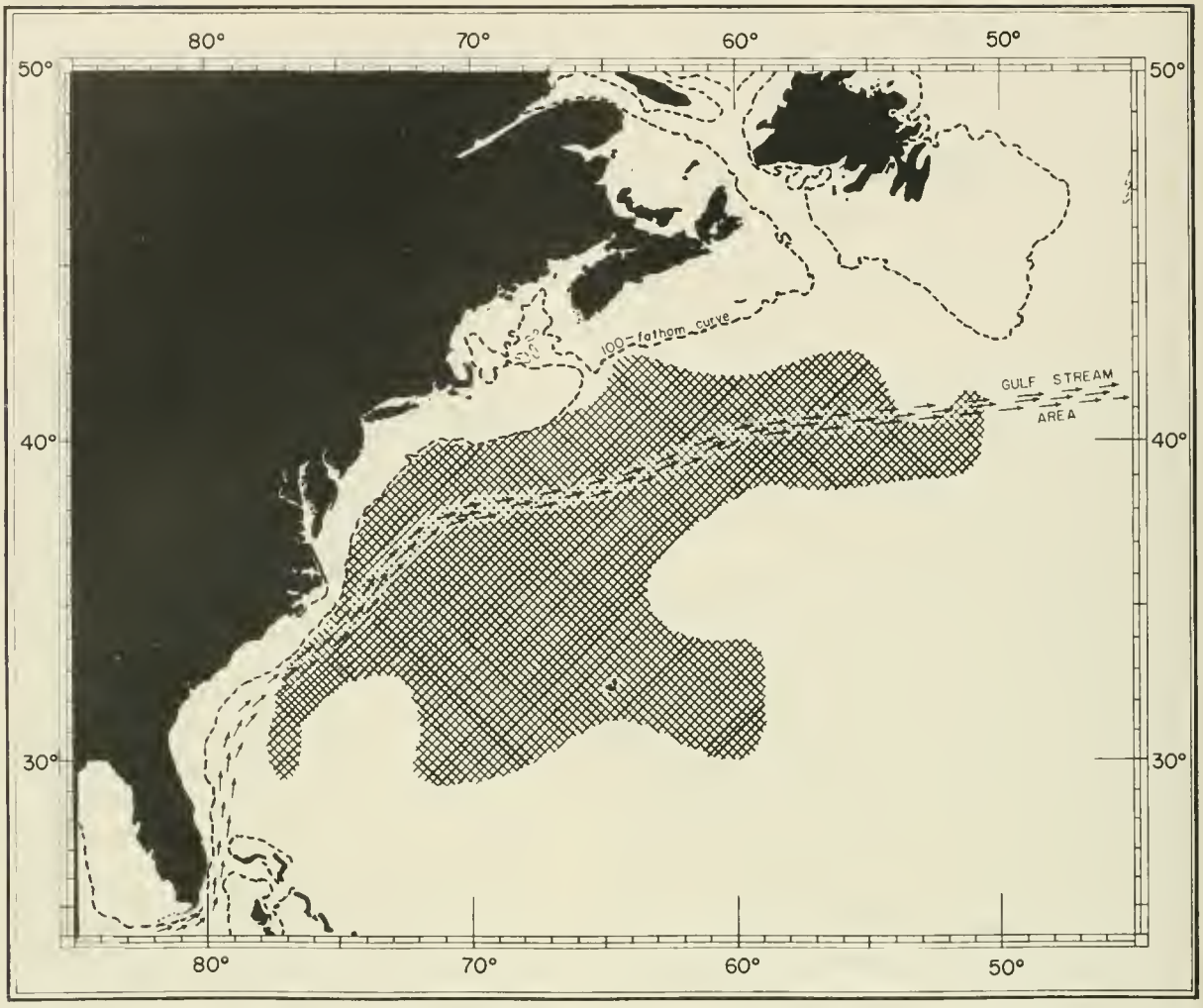

FIGURE 1.—Oceanic region of the northwestern Atlantic covered in M/V *Delaware* tuna explorations, 1957–60.

THE STATUS OF TUNA KNOWLEDGE, 1957

A review of the literature indicated that no knowledge was available of extensive tuna stocks in the oceanic region of the northwestern Atlantic and that records of tuna captures in this region were relatively few. The review showed further that whereas knowledge of tuna stocks of the Continental Shelf was more extensive, it was confined almost entirely to the period during which these stocks are available to fishermen, roughly June or July through October. Knowledge of the tunas of the shelf had been provided largely by commercial and sport fishermen and through explorations conducted by the Bureau and the Woods Hole Oceanographic Institution.

Information on the hydrography of the oceanic region also was examined and analyzed, and inquiries concerning sightings of tuna schools at the surface were made with the U.S. Coast Guard and the Woods Hole Oceanographic Institution. Answers to these inquiries and the scarcity of school sightings during a 1956 cruise of the *Delaware* were discouraging and indicated that little surface-fish life exists in the Gulf Stream area—an indication that was later substantiated.

In general the outlook was discouraging; however, there was one favorable sign. Mowbray (1956) in the Bermuda area in the mid-1950's had successfully used drifted longline gear to capture four species of tunas—bluefin, yellowfin, albacore, and little tuna. These results suggested

that tunas were to be found in subsurface rather than surface waters of the oceanic region. Largely for this reason, the *Delaware* explorations were conducted with longline gear.

A brief review of the knowledge of each tuna species known to inhabit the northwestern Atlantic follows. This review portrays the status of knowledge of the tunas of Continental Shelf and the oceanic regions prior to the start of *Delaware* explorations in 1957.

BLUEFIN TUNA

Bluefin, largest of the tunas, are common on the Continental Shelf off eastern United States and Canada from June through October. Because of their large size, bluefin are considered highly desirable game fish and have dominated tuna catches of the shelf sport fishery for many years (Westman and Neville, 1942). The species has also dominated the commercial fishery. Commercial purse seining for bluefin tuna existed in the late 1930's in the Continental Shelf area north of Cape Cod (Murray, 1952), and limited commercial bluefin production was achieved through trapping, sporadic seining, harpooning, and hook-and-line fishing in the 1940's and early 1950's. In efforts to help the fishery, the Bureau conducted gear trails on the shelf in 1951 and 1954 with Pacific coast purse seine gear and techniques (Murray, 1952, 1955) and in 1952–53 with longlines (Murray, 1953, 1954). The Woods Hole Oceanographic Institution, Miami Marine Laboratory, and the Bureau have been engaged in studies of the life history of bluefin for several years (Mather, 1959; Rivas, 1954, 1955; Robins, 1957; Westman and Gilbert, 1941; and Westman and Neville, 1942).

Bluefin had also been reported from near Bermuda by Mowbray,[1] but no records of this species in the oceanic region adjacent to the coast of North America existed prior to the *Delaware* work.

Migratory routes taken by bluefin on their way to and from their summer habitat in the inshore areas and the location of their winter habitat have long been subjects of considerable speculation among fishermen and fishery biologists. The most popular view has been that in the fall when the fish head south or southeast into the oceanic region, toward unknown spawning grounds, probably in the Caribbean Sea. Bullis and Mather (1956), through examinations of bluefin ovaries, have partially substantiated the supposition that the spawning grounds, for at least part of the bluefin population, lie in the Caribbean. The migration route may lead directly to the spawning grounds or may be circuitous. Other workers proposed that bluefin could perhaps winter in deeper waters along the Continental Slope off the Middle Atlantic States (Bigelow and Schroeder, 1953).

The return migration has been linked with an observed northward migration of large tuna in mid-May and June along the western edge of the Straits of Florida. Rivas (1951, 1954) proposed that these migrants comprise the stock of large fish that enter the New England and Nova Scotia fisheries in late June. Rivas later (1955) stated that the fish taking part in this migration ranged from 300 to 700 pounds and averaged 400 to 500 pounds. Linking these fish with those of the northern inshore fishery would, if confirmed, account for the large individuals, but this would still leave unexplained the many small bluefin common to the northern fishery.

YELLOWFIN TUNA

Yellowfin tuna are not common inhabitants of the Continental Shelf areas and are less well-known in the northwestern Atlantic than bluefin. One yellowfin was taken on a trolling line from the Bureau research vessel *Theodore N. Gill* in February 1953 (Anderson, Gehringer, and Cohen, 1956), north of the Bahamas. In the true oceanic region between the Continental Slope of North America and Bermuda, five additional records exist—all from trolling line captures. One of these refers to a fish taken in 1949 by the Woods Hole Oceanographic Institution research vessel *Caryn* and two to yellowfin taken in 1953 by the WHOI research vessel *Atlantis* (Mather and Gibbs, 1957); and two to fish taken in 1954 by the *Atlantis* (Mather, 1954). Yellowfin also were reported from the Bermuda area by Mowbray (1956).

ALBACORE

Albacore have been reported by Goode and Bean (1879) off Woods Hole and near Banquereau Bank off Nova Scotia. One specimen was reportedly taken by a halibut trawl off Devil's Island

[1] Mowbray, Louis S. The gamefishes of Bermuda. Paper presented at the International Gamefish Conference, International Oceanographic Foundation, Nassau, 1956, 8 p.

near Halifax harbor in 1922 (Vladykov, 1935), and one was captured by the Woods Hole Oceanographic Institution research vessel *Bear* at latitude 39°45′ N., longitude 73°00′ W. in September 1956 (Mather and Gibbs, 1957). In addition, albacore have been taken on longline gear around the island of Bermuda by Mowbray (1956). Other reports of albacore captures exist but are unconfirmed.

BIGEYE TUNA

Captures of bigeye tuna have been reported from sport fishery catches on the Continental Shelf off North Carolina and Maryland, and Mowbray (1956) has recorded the capture of bigeye off Bermuda. The species was unrecorded from the oceanic region off the United States and Canada prior to the Bureau's exploratory studies.

OTHER TUNA SPECIES

Blackfin tuna are recorded from the Bermuda area by Mowbray (1956) and from oceanic waters of the northwestern Atlantic by Mather and Day (1954). One of the two specimens constituting the latter record was taken near latitude 32°21′ N. and longitude 64°37′ W. by the *Atlantis* in June 1948. The other specimen was taken 300 miles east of Cape Hatteras by the same vessel in August 1953. A number of specimens has been taken in inshore areas, and Mather (Mather and Day, 1954) believes that the species does not normally range far beyond the 100-fathom curve. The northernmost record of the species is the capture of one blackfin about 75 miles south of Martha's Vineyard (latitude 40°04′ N., longitude 70°42′ W.) by the *Caryn* in October 1948 (Mather and Schuck, 1952).

Little tuna are common inhabitants of inshore areas, especially from New York south, and have been reported from the Gulf of Maine by Schuck (1951). Little tuna do not, apparently, range into deep waters. Sporadic attempts have been made, along the Middle Atlantic coastline, to utilize little tuna commercially.

EXPLORATORY GEAR AND PROCEDURES

The Bureau research vessel *Delaware* traveled over 17,900 nautical miles during the explorations in the northwestern Atlantic (fig. 2).

FISHING GEAR

The longline fishing gear used in the explorations (fig. 3) is identical in basic design and construction to that used by the Bureau research vessel *Oregon* in exploring the tuna resources of the Gulf of Mexico (Captiva, 1955) and Caribbean. The method of longlining used by the *Delaware* was essentially the same as that used by the Japanese for tuna fishing operations in the Pacific, Indian, and Atlantic Oceans.

FISHING PROCEDURE

On station, the fishing gear and bait were prepared for setting at about 0630 hours. A set of 60 tubs of longline gear (600 hooks) was selected, following initial operations, as the unit that would give a reasonable representation of fish in the area, but this set would still be convenient to handle when large numbers of large fish were caught. Atlantic herring, *Clupea harengus harengus* Linnaeus, were used as bait. The gear was allowed to drift for about 2 hours after the last tub had been set, and hauling was then begun with the aid of a Japanese longline hauler. The vessel was moved slowly ahead as the gear was being retrieved so that the line was kept on the starboard quarter. When a fish was brought to the side of the vessel, the branchline bearing the fish was removed from the mainline, another branchline was tied on, and hauling was continued. The fish, on its separate branchline, was then gaffed and hauled aboard or tagged and released. Tagging was carried out in cooperation with the Woods Hole Oceanographic Institution. Setting the gear required four to five men; retrieving it required six to seven.

TEMPERATURE DETERMINATIONS

Several workers (Murphy and Shomura, 1955; Bullis, 1955; and Wathne, 1959) have stated that longline sections do not function with uniform efficiency or at uniform depth, owing to the many variables to which the gear is subjected. These variables include lengths of mainline, branchlines, and buoylines, as well as the amount of tension applied to the mainline when the gear is set, the force and direction of the wind, and the strength and direction of the current.

FIGURE 2.—The M/V *Delaware*, 148-foot exploratory research vessel, owned and operated by the Bureau of Commercial Fisheries.

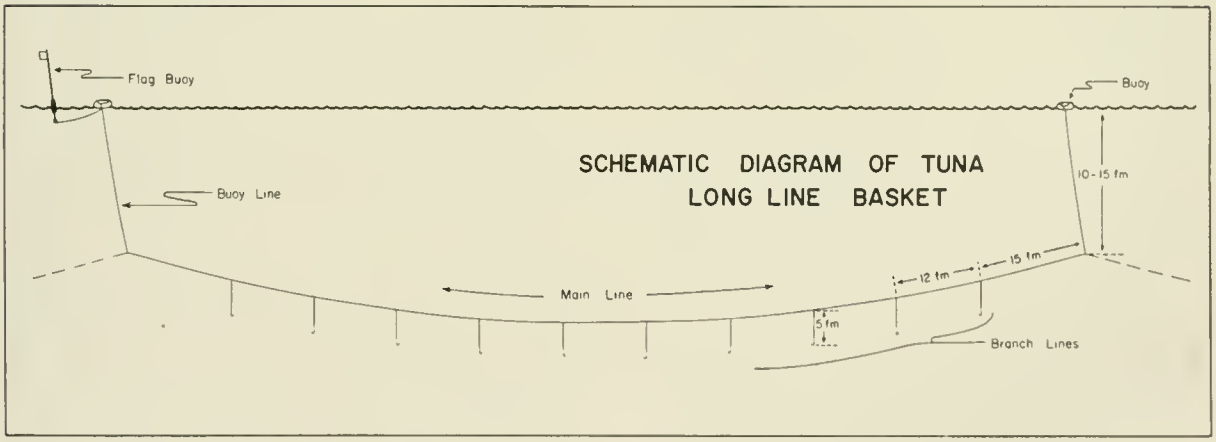

FIGURE 3.—Schematic diagram of the tuna longline gear used in *Delaware* explorations.

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Since there are so many variables operating on a longline, determination of the depth at which the hooks were situated (estimated average fishing depth) is based on calculations taken from echograph observations of similar gear by Bullis (1955) and Wathne (1959). These calculations showed that, with the gear used, the average hook was placed at a depth of about 173 feet.

At all fishing stations a bathythermograph cast was made to a minimum depth of 450 feet. Water temperatures at the surface and at the 173-foot estimated fishing depth were obtained from these casts, and within the limits of the data, temperature ranges and average water temperatures were determined for tuna of each species.

DISTRIBUTION OF EXPLORATORY EFFORT

Explorations were carried out as one phase of the overall program of the North Atlantic Fisheries Exploration and Gear Research Base. Fishing effort was distributed through all seasons, but it was necessarily intermittent. In all, eight cruises were devoted to tuna exploration and 111 stations were fished with longline gear. Of the 111 stations, 9.9 percent were fished in winter (January and February), 37.8 percent were fished in spring (March, April, and May), 14 percent in early summer (June), 18.5 percent in middle and late summer (July and August), and 19.8 percent in fall (September and October). No stations were fished in November or December.

The first cruise in the oceanic region was designed to cover the entire region. The vessel route ran south from the 1,000-fathom curve off New England to the approximate latitude of Cape Hatteras, then east past Bermuda, and north to the point of origin. The cruise took place in the early spring, for the cruise objective was to intercept, and record the distribution of bluefin tuna during a portion of the spring migration. The seven cruises that followed were carried out to cover areas where tuna had been concentrated on previous cruises or where the possibility of tuna concentrations had been indicated by hydrographic data or theories on migration routes, and to cover systematically the Gulf Stream area with a series of longline sets, 95 to 120 miles apart.

PHYSICAL CHARACTERISTICS OF THE REGION EXPLORED

The oceanic region explored by the *Delaware* extends south and east of the edge of the Continental Shelf of northeastern North America to about latitude 30° N. and longitude 50° W. The region is characterized by the presence of that portion of the Gulf Stream system known as the Gulf Stream proper. Since the region is influenced greatly by the Gulf Stream system, an understanding of the physical nature of the system is a necessary preliminary to an understanding of the distribution of that region's fauna.

The Gulf Stream system is composed of three principal parts: the Florida Current from the Tortugas to Cape Hatteras; the Gulf Stream proper from Cape Hatteras to the Grand Banks; and the North Atlantic Current from the Grand Banks eastward. As the principal current system of the western North Atlantic, the Gulf Stream system is analogous to the Kuroshio Current of the western North Pacific. It has been studied in detail by the Woods Hole Oceanographic Institution, and as a result, considerable information is available that relates directly to a study of the environmental conditions that may affect the distribution of the tunas.

The Gulf Stream system is described by Stommel (1960) as:

> . . . a narrow, intense, northeastward–flowing current which returns to the north again the southward–driven Sargasso Sea water that has passed through the Caribbean and has turned through the Florida Straits. The Gulf Stream flows along the western boundary of the warm Sargasso Sea surface water. As the Stream turns toward the east, off the Grand Banks, it acts as a kind of dynamic barrier, or dam, which, by virtue of coriolis forces, restrains the warm Sargasso Sea water from overflowing the colder northern water of the North Atlantic. The water in the Stream is not significantly different in temperature from the large mass of warm water which lies to the right of its direction of motion.

Studies have shown that variations occur within the Gulf Stream system in the form of wavelike perturbations that can be likened to the meanders of a geologically old river or stream, and other physical complications occur along the edge of the Stream in the form of cyclonic eddies (Iselin, 1960). Then too, the water masses of the Gulf

Stream frontal area, which occur between the Gulf Stream axis and the cooler waters to the north, are not stable. They have been described by von Arx, Bumpus, and Richardson (1955) as having ". . . a structure which, as far as one can tell, is best interpreted as a succession of short, overlapping segments which may be described as 'shingles'." The "shingle effect" is of left-hand orientation as one looks down the axis of the Gulf Stream system.

Bathythermograph recordings indicate that relatively large variations in temperature occur within short distances in the oceanic region lying on either side of the Gulf Stream. On several cruises, bathythermograph casts were made at each end of the longline set, and even in this relatively short distance, marked variations in temperature were observed.

The Gulf Stream, south of New England, effectively divides the region investigated into a cool-water northern area and a warm-water southern area.

DISTRIBUTION OF DOMINANT TUNA SPECIES

EXPLORATORY RESULTS AND OBSERVATIONS

Catch rates, for the entire investigation and for all species of tuna, ranged from no tuna at several stations to a high figure of 20.8 tuna per 100 hooks. Catch rates and catch composition varied widely with season and geographical area fished (figs. 4–8), as did the weights of individual fish (table 1).

Bluefin Tuna

The single exploratory cruise conducted in winter indicated that bluefin tuna are common in the portion of the oceanic region lying east of the Continental Shelf, from Cape Hatteras to south of New England (fig. 4A). The extent of the bluefin population to the north and east toward the Grand Banks during winter and late fall is unknown. The greatest number of bluefin in winter were caught along the northern edge of the Gulf Stream (fig. 4A) where, at one station, the catch rate was 5.7 bluefin per 100 hooks. The fish caught at this station averaged nearly 300 pounds each, although large fish apparently are not common in winter, in the area investigated.

The distribution pattern assumed by bluefin in spring (fig. 5A) is similar to that in winter, at least in the portion of the region explored in both seasons; and exploratory catches indicate that commercial longline fishing might be feasible in the vicinity of the Gulf Stream in spring, and possibly in winter. Bluefin were taken in spring at the easternmost stations occupied, south of Grand Banks and east of Bermuda. Highest catch rates were achieved farther south and west of these stations, however, in the general area of the Gulf Stream (fig. 5A). At one station, south of Cape Cod on the inshore side of the Gulf Stream, the catch rate was 16.3 bluefin per 100 hooks. Almost directly east of that station, on the northern edge of the Stream, the maximum catch rate for the entire series of cruises was attained—20.8 bluefin per 100 hooks.

TABLE 1.—*Estimated weights of tunas, by seasons*

Season [1]	Major species [2]								
	Bluefin			Yellowfin			Albacore		
	Number	Total weight	Average weight	Number	Total weight	Average weight	Number	Total weight	Average weight
		Pounds	*Pounds*		*Pounds*	*Pounds*		*Pounds*	*Pounds*
Winter	100	19,901	199	18	589	33	17	554	33
Spring	687	107,287	156	213	18,546	87	31	1,242	40
Early summer	82	28,270	345	50	5,321	[3] 106	8	268	34
Summer	6	1,428	238	109	10,733	98	15	750	50
Fall	2	650	325	329	17,325	53	42	1,990	47
Totals	877	157,536		719	52,514		113	4,804	
Averages			253			75			41

[1] Seasons are defined as follows: Winter=January, February; spring=March, April, May; early summer=June; summer=July, August; fall=September, October. No explorations were conducted in November or December.

[2] Average weights of species of minor importance are: Bigeye, 137 pounds; skipjack, 18 pounds; blackfin, 13 pounds.

[3] Reflects a large catch of fish made at one station.

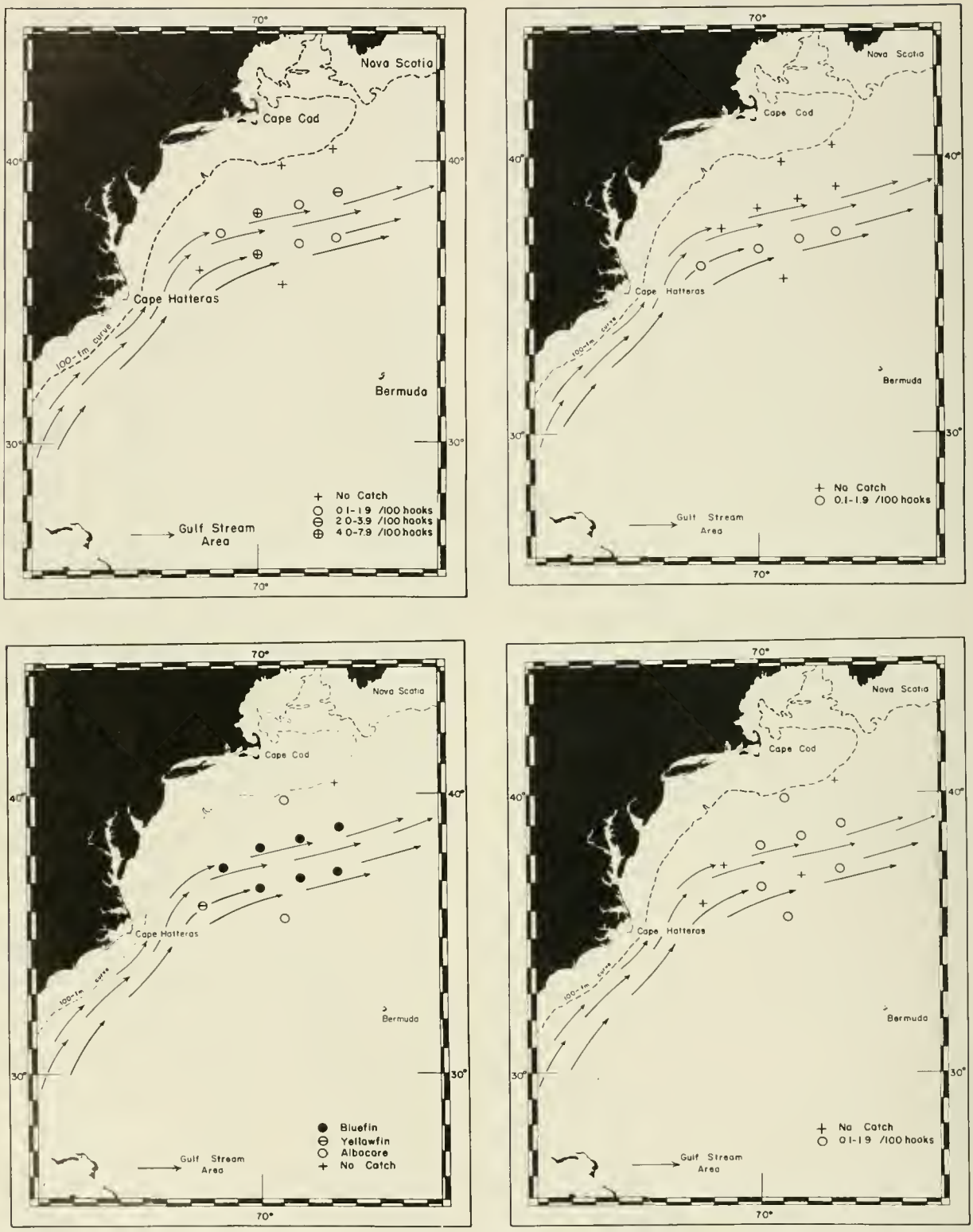

FIGURE 4.—Observed distribution of dominant tuna species in winter (January and February), based on *Delaware* cruise 59–1.

Upper left—Bluefin. Upper right—Yellowfin. Lower left—All dominant species. Lower right—Albacore.

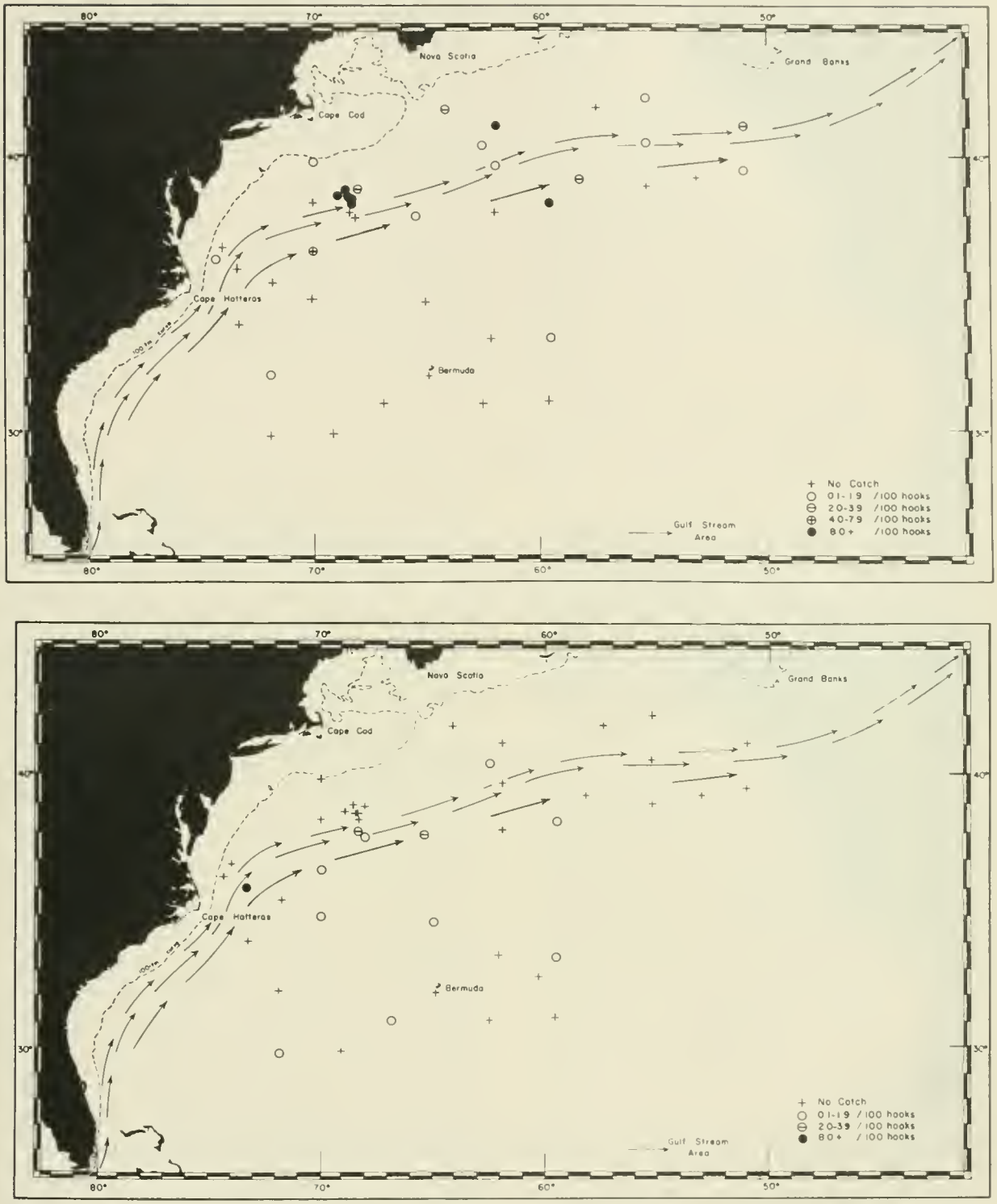

FIGURE 5.—Observed distribution of dominant tuna species in spring (March, April, and May), based on *Delaware* cruise, 57–3, 58–2, 59–6, 60–6.

Upper—Bluefin. Lower—Yellowfin.

FIGURE 5.—Observed distribution of dominant tuna species in spring (March, April, and May), based on *Delaware* cruise, 57–3, 58–2, 59–6, 60–6.

Upper—All dominant species. Lower—Albacore.

Although bluefin caught during the spring were mostly small, several weighed over 300 pounds and one, caught east of Bermuda, was estimated to weigh between 350 and 400 pounds.

By late spring or early summer (fig. 6A), bluefin begin to disappear from the oceanic region, and by midsummer (fig. 7A) are uncommon. They apparently remain scarce in oceanic waters through early fall (fig. 8A).

The range of water temperatures in which bluefin were taken during the explorations and the average water temperature for all stations at which bluefin were taken are shown in figure 9. The mean temperatures were obtained by using the following formula:

$$\bar{x}=\frac{(f\times t)}{N}$$

where f=the number of fish in a sample; t= water temperature in degrees F.; and N=the total number of fish of each species for which data were available.

Yellowfin Tuna

Yellowfin tuna apparently do not occur in large numbers anywhere in the oceanic region of the northwestern Atlantic in winter, and none were taken north of the Gulf Stream during that season (fig. 4B).

In the spring the fish are widely distributed over the southern portion of the region, but explorations indicate that they are not generally present in large concentrations. However, at one station, east of Cape Hatteras near the Gulf Stream axis, yellowfin were caught at the rate of 14.1 fish per 100 hooks (fig. 5B).

In summer and fall (figs. 6B–8B), the fish were found in greater general concentration, especially in the vicinity of the Gulf Stream. The highest catch rate achieved during explorations in the summer was 5.0 yellowfin per 100 hooks, and the highest catch rate in the fall was 8.5 yellowfin per 100 hooks. A wide variation in weight was noted among yellowfin caught at stations fished in different areas and seasons. For instance, at a station fished in July in the area north of the Gulf Stream the fish averaged only 30 pounds, whereas in April at a station farther south the fish averaged 92 pounds.

The observed range of water temperature and the average temperature of the water inhabited by yellowfin taken during the explorations are shown in figure 9.

Albacore

Albacore appear to be widely distributed, but thinly scattered, in the oceanic region in all seasons (figs. 4D–8D), and no specific patterns were discerned, either of migration or distribution. The maximum albacore yield, from a longline set, was at the rate of 2.0 fish per 100 hooks. Many of the albacore taken were large, and the average weight for all albacore taken at all stations was 41 pounds. Observed temperature limits and averages for albacore are shown in figure 9.

Other Tuna Species

In addition to the dominant species for which the distribution has been described, several other species, of lesser importance, were taken. These included skipjack and bigeye. Individuals of these species, however, were taken so rarely and in such small numbers that little can be said concerning their patterns of distribution on the basis of the *Delaware* explorations. Some of the stations at which bigeye were caught are shown in figure 7C and represent the northernmost records of the species for the western North Atlantic (Mather and Gibbs, 1958). The temperature range of waters in which bigeye were caught is shown in figure 9.

DISCUSSION

Although the exploratory coverage was not complete, owing to the intermittent scheduling necessitated to carry out several other program phases during the period of investigation, the outline of distribution of bluefin and yellowfin tunas that emerges does provide a substantial basis for future work and a more complete understanding than was formerly available.

Workers in Japan (Nakamura, 1951; Nakamura, Yabuta, and Mimura, 1956; Uda, 1953) and the United States (Sette, 1955) have established that concentrations of tuna are generally associated with oceanic, convergent, tropical, and subtropical water masses—particularly those of major circulatory systems. Extensive work in the Pacific has resulted in the discovery of definite correlations between tuna abundance and the major circulatory systems of the Kuroshio or North Pacific Current, the North and South Equatorial Currents, and the counter currents to these.

FIGURE 6.—Observed distribution of dominant tuna species in early summer (June), based on *Delaware* cruise 57–5.

Upper left—Bluefin. Upper right—Yellowfin. Lower left—All dominant species. Lower right—Albacore.

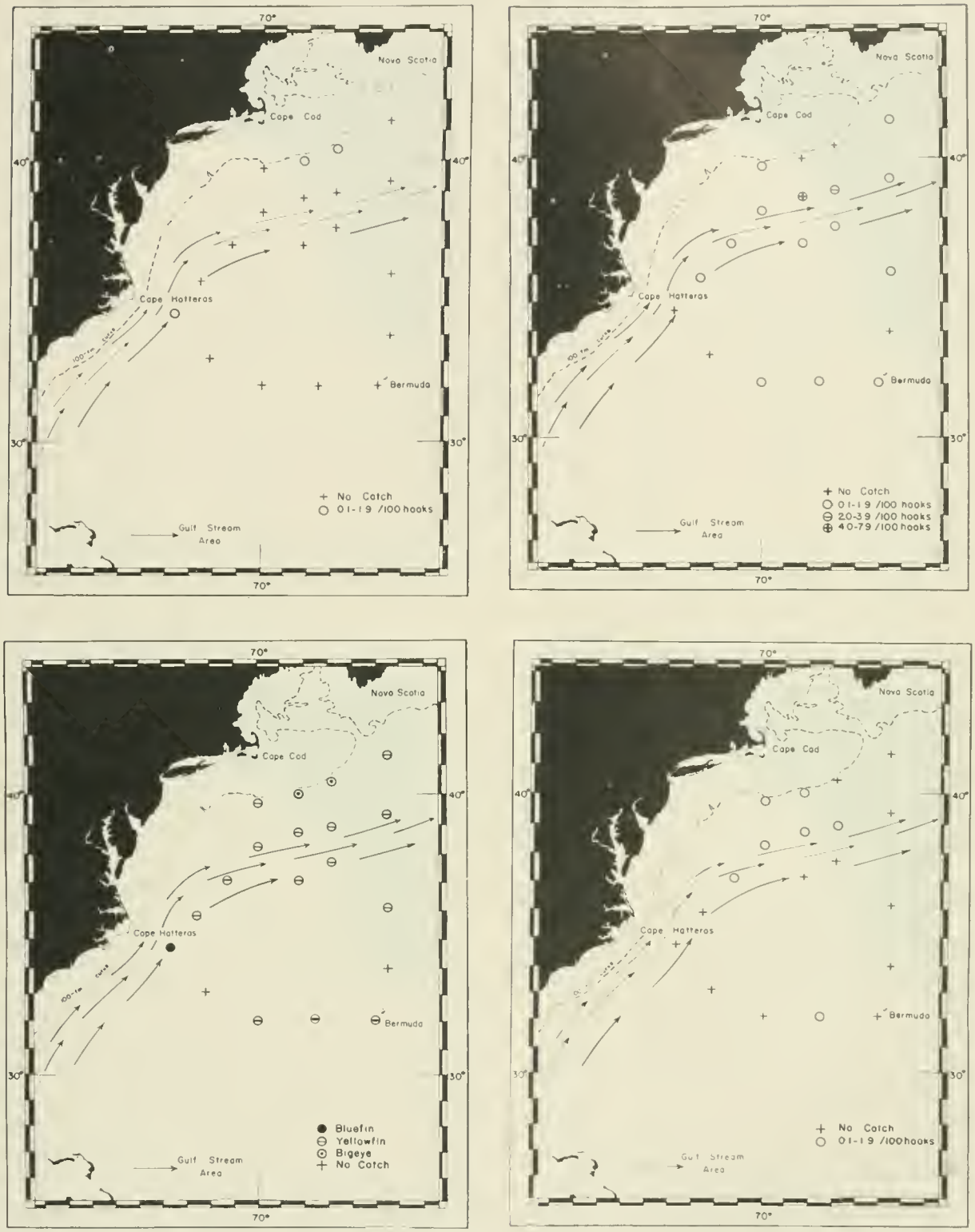

FIGURE 7.—Observed distribution of dominant tuna species in middle and late summer (July and August), based on *Delaware* cruise 57–5, 58–3.

Upper left—Bluefin. Upper right—Yellowfin. Lower left—All dominant species. Lower right—Albacore.

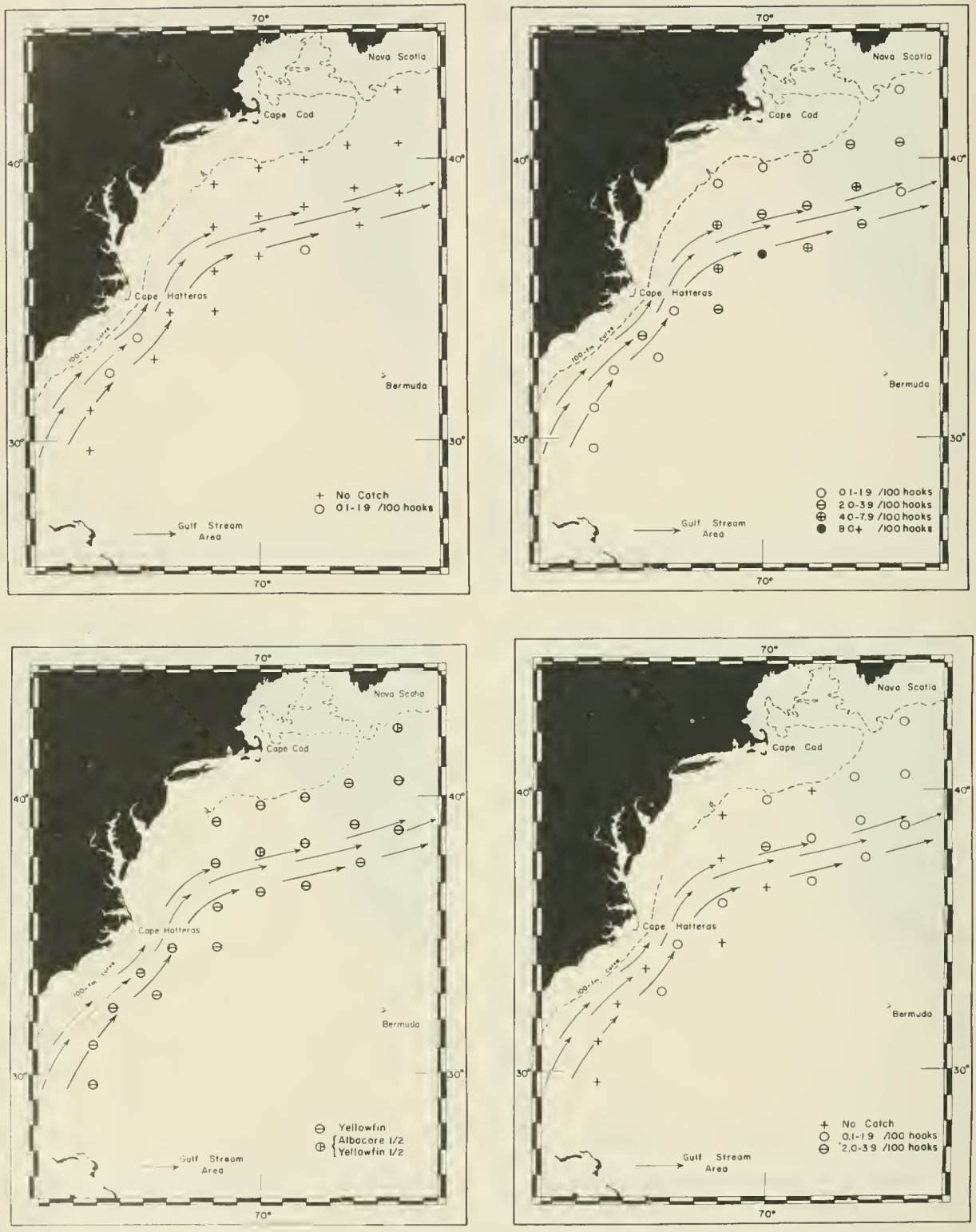

FIGURE 8.—Observed distribution of dominant tuna species in fall (September, October, and November), based on *Delaware* cruise 57-8.

Upper left—Bluefin. Upper right—Yellowfin. Lower left—All dominant species. Lower right—Albacore.

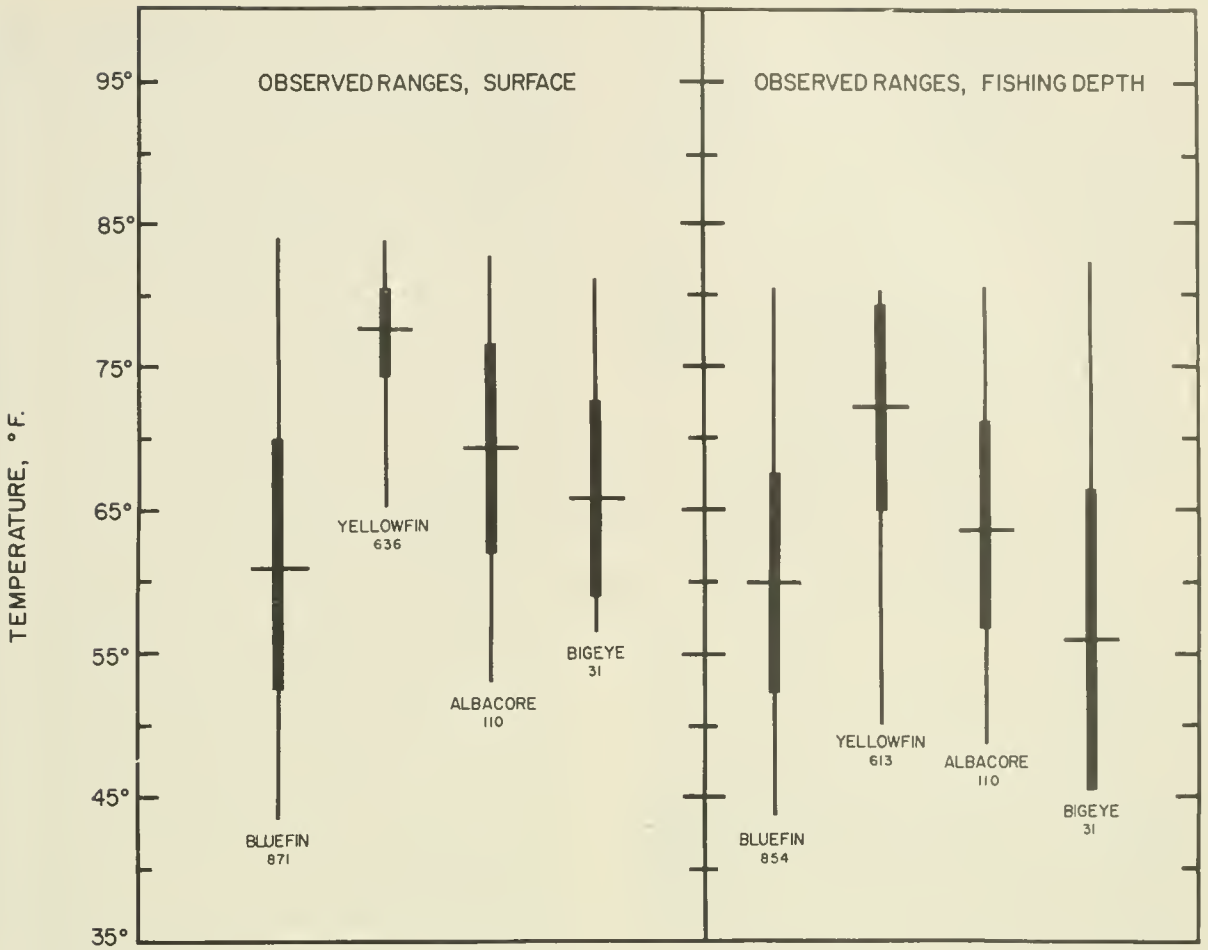

FIGURE 9.—Temperature ranges and mean temperatures for four species of tunas. Data based on temperatures recorded at stations where tunas were captured. The thin line represents the total recorded temperature range; the thick line represents 1 standard deviation on either side of the mean; and the cross bar represents the mean. The number of tunas used in the calculations are recorded below the species names.

Further, the areas yielding the greatest abundance of tuna have generally been found near the boundaries of these systems. In many cases the abrupt temperature gradients present at the edges of frontal zones of the current systems serve to separate the environments on either side of the gradients to such an extent that tuna of two or more species (for instance bluefin and yellowfin) may exist within a short distance of one another and yet be distinctly separated.

Delaware explorations indicate that temperature is an important environmental key to species distribution in the north frontal area of the Gulf Stream. To illustrate the close geographical proximity of tuna of one species to those of another in the presence of a temperature gradient, two series of isotherms were plotted from temperature recordings made at tuna stations in and near the Gulf Stream frontal area (fig. 10). The resulting plots represent conditions over a period of several days. Despite the rapidity with which individual points in the frontal area may change temperature, the general temperature structure represented should remain essentially the same, and the way in which two species—with differing ecological requirements—can exist as dominants in close proximity is indicated. Fishing results at the same points show clearly the definite change in species composition, from bluefin in the cooler waters on the edge of the Gulf Stream to yellowfin in the warmer waters in the Gulf Stream. This change in species composition with change in tem-

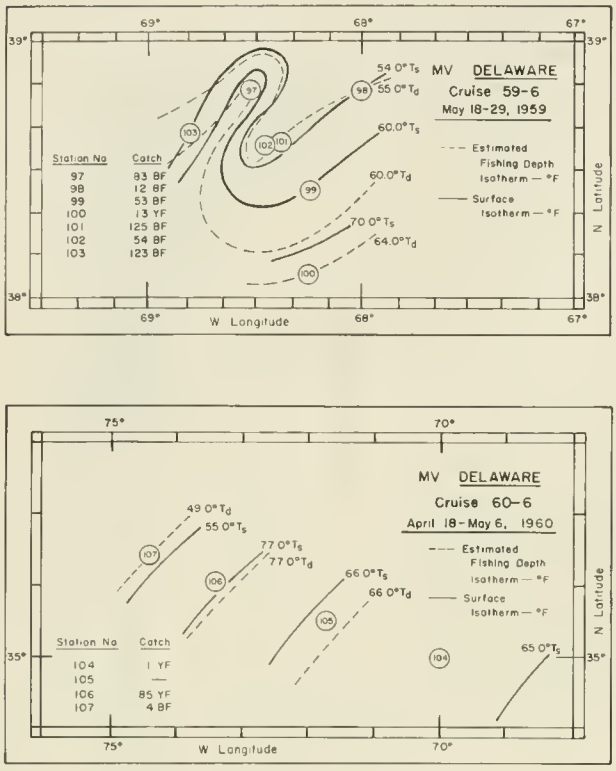

FIGURE 10.—Effect of a temperature gradient in allowing the presence of two ecologically dissimilar tuna species, bluefin (BF) and yellowfin (YF), in close proximity. Lines represent isotherms; numbered circles on lines represent the position of fishing stations with respect to the temperature. Station 100 (upper figure) was fished directly in the axis of the Gulf Stream.

perature was indicated throughout the investigation.

A comparison of the weighted average temperature of the water at stations where bluefin and yellowfin were caught (fig. 9) provides additional evidence that bluefin prefer areas of cooler water and are most abundant in cool-water areas despite the wide spread of temperatures (36° F.) included within the range observed for this species.

In early summer, when the bluefin begin to migrate from the oceanic areas, the occurrence of bluefin is reported, each year, on the Continental Shelf. This and evidence obtained from tagging tend to indicate that at least a part of the bluefin tuna of the New England and Nova Scotia summer fishery migrate to the Continental Shelf from the Gulf Stream area. One tuna, captured and tagged by the *Delaware* on May 24, 1959, 325 miles east of Ocean City, Md., was recaptured in a commercial purse seine near Cape Cod about 3 months later. But earlier evidence from tagging work accomplished by the Woods Hole Oceanographic Institution on the Continental Shelf indicates that tuna make transoceanic migrations (Mather, 1960). It is not unreasonable to suppose, therefore, that part of the tuna that winter near the Gulf Stream migrate to more distant waters than the waters of the nearby Continental Shelf. Nor is it unreasonable to suppose that at least part of the tuna found on the Continental Shelf of New England and Canada in summer months have migrated from points farther distant than the Gulf Stream area, as would be necessary if the popular theory that the large fish winter in the Caribbean were confirmed.

The available temperature data show that mean surface temperatures at the Boston light vessel ranged from 53.7° to 64.2° F. during the summer of 1957 (Day, 1959). The weighted average temperature of 59.9° F., that was calculated for oceanic stations yielding catches of bluefin tuna near the Gulf Stream (fig. 9), is within this range. Migration of bluefin into the shelf area from oceanic stations in late spring or early summer would, therefore, be accompanied by only minor temperature changes.

In contrast, Rivas (1955), in his discussion of the possible migration of bluefin from the Straits of Florida to the Gulf of Maine, stated " . . . they go in two to three weeks from temperatures of 28 to 29 degrees centigrade into waters which are 16 to 18 degrees centigrade." (From 82° to 84° F. to 61° to 64° F.) This spread of 18° to 23° represents a much greater change than would be faced by fish moving into the Gulf of Maine from the Gulf Stream area to the north, but seems to be well within the realm of possibility.

The explorations indicate that the early summer period, marking the migration of the bluefin from the oceanic area north of the Gulf Stream, also represents a period of transition in species dominance in that region. As the bluefin, which have been the dominant tuna through the winter and spring, migrate from the area, yellowfin appear and assume dominance through the summer (figs. 4C–8C).

The migratory patterns assumed by the yellowfin during this spring-summer shift and the routes taken have not been observed; but, on the basis

of the evidence available, the fish are assumed to migrate from the general oceanic area south of the Gulf Stream. Yellowfin are seldom reported from inshore areas along the east coast, and confirmed records are nonexistent for the New England inshore area. However, I received an unconfirmed report of two yellowfin being taken with longline gear on Middle Bank, south of Gloucester, Mass., during the summer of 1959. Captures of the species in winter and spring have all been made in the southern areas. The yellowfin captured north of the Bahamas by the *Theodore N. Gill* in February 1953 (Anderson, Gehringer and Cohen, 1956) and the catch rate of 14.1 yellowfin per 100 hooks in the Gulf Stream east of Cape Hatteras in May provide evidence to support the assumption of migration from oceanic areas in the southern portion of the region.

Temperatures recorded at the fishing depth of the longline gear at stations in the northwestern Atlantic where yellowfin were caught compare favorably with surface water temperatures at stations in the eastern Pacific where surface-dwelling yellowfin were caught. Surface temperatures were recorded during extensive tuna-tagging operations conducted from 1952–59 by the California Department of Fish and Game, and temperature data were made available by Blunt and Messersmith (1960) for localities at which tuna were tagged that were later recovered. Using these data, a weighted average temperature of 71.4° F. was calculated for surface-caught yellowfin in the eastern Pacific. This is closely comparable to the weighted average of 72.1° F., calculated for water depths at which the subsurface yellowfin of the northwestern Atlantic were caught.

OTHER INHABITANTS OF THE OCEANIC REGION

In addition to tunas, fishes belonging to several other species were taken by the longline gear (table 2). Many of these were little-known species in the oceanic northwestern Atlantic prior to *Delaware* explorations.

Sharks were taken at a high percentage of longline stations, and their presence is important in evaluating the commercial potential of oceanic longlining in an area, because longline-caught tuna may be damaged to varying degrees by sharks. Shark damage to individual tuna may vary from minor superficial damage to complete loss. Tunas having minor damage are in most cases acceptable to the canning industry. Percents given in the following paragraphs represent only the occurrence of shark damage, not the severity of the attack. During explorations in the northwestern Atlantic, 4.2 percent of the tuna caught were reported damaged by sharks. In explorations in the Gulf of Mexico, 13.6 percent of the yellowfin tuna that were caught were damaged to varying degrees (Wathne, 1959), and the Pacific Oceanic Fishery Investigations recorded 20-percent damage for yellowfin in the Line Islands area (Iversen and Yoshida, 1956).

In the oceanic areas near the Gulf Stream where bluefin tuna were taken in relatively large quantities, very little shark damage occurred. Damage ranged from zero to a high of 12.5 percent at stations yielding large quantities of bluefin. There was no shark damage at stations fished during cruise 59–7, even though approximately 35 tons of bluefin were caught. More yellowfin have been damaged by sharks in the Gulf Stream area, however, than bluefin, and the percentage of damaged yellowfin appears to be comparable to that of other oceanic areas. Damage ranged from zero to 20.6 percent of the fish caught.

All the species of sharks responsible for tuna damage are not known. Sharks observed as they attacked tuna being hauled to a point near the surface were usually whitetips, *Carcharhinus longimanus* (Poey). Whitetip sharks are also suspected of damaging tuna in the Gulf of Mexico

TABLE 2.—*Species taken on longline gear in the oceanic northwestern Atlantic during Delaware explorations*

Family	Scientific name	Common name
Lamnidae	*Isurus oxyrinchus* Rafinesque	Mako.
	Lamna nasus (Bonnaterre)	Porbeagle.
Carcharhinidae	*Carcharhinus floridanus* Bigelow	Silky shark.
	Carcharhinus longimanus (Poey)	Whitetip shark.
	Carcharahinus obscurus (LeSueur)	Dusky shark.
	Carcharhinus falciformis (Muller and Henle)	Sickle shark.
	Prionace glauca (Linnaeus)	Blue shark.
Sphyrnidae	*Sphyrna* sp.	Hammerhead shark.
Alepisauridae	*Alepisaurus ferox* Lowe	Longnose lancetfish.
	Alepisaurus brevirostris Gibbs	Lancetfish.
Lampridiidae	*Lampris regius* (Bonnaterre)	Opah.
Coryphaenidae	*Coryphaena hippurus* Linnaeus	Dolphin.
Bramidae	*Taractes longipinnis* (Lowe)	Bigscale pomfret.
Scombridae	*Acanthocybium solanderi* (Cuvier)	Wahoo.
	Euthynnus pelamis (Linnaeus)	Skipjack tuna.
	Thunnus alalunga (Bonnaterre)	Albacore.
	Thunnus albacares (Bonnaterre)	Yellowfin tuna.
	Thunnus atlanticus (Lesson)	Blackfin tuna.
	Thunnus obesus (Lowe)	Bigeye tuna.
	Thunnus thynnus (Linnaeus)	Bluefin tuna.
Istiophoridae	*Makaira albida* (Poey)	White marlin.
	Makaira nigricans Lacépède	Blue marlin.
Xiphiidae	*Xiphias gladius* Linnaeus	Swordfish.

(Bullis, 1955; Backus, Springer, and Arnold, 1956). Other sharks probably also attack the line-caught tuna.

SUMMARY

From 1957–60, tuna explorations were carried out, intermittently, to determine the distribution of tunas in the oceanic portion of the northwestern Atlantic and to assess the availability of tunas to commercial gear. Major effort was expended in the Gulf Stream proper. Longline gear, fished from the Bureau vessel *Delaware* at 111 stations, caught bluefin, yellowfin, albacore, skipjack, and bigeye tunas.

Temperature studies show that the Gulf Stream system provides the environmental conditions favorable for the presence of tunas in the oceanic portion of the northwestern Atlantic. Bluefin, preferring cooler water, are the dominant tuna in the vicinity of the Gulf Stream in winter and spring. Longline catches indicate that a commercial fishery for bluefin might be profitable in those seasons. Bluefin disappear from the oceanic region in late spring or early summer, and yellowfin, preferring warmer water, are the dominant tuna in summer and fall.

A sharp temperature gradient on the edge of the Gulf Stream allows tunas of two or more species with dissimilar temperature requirements to exist within short distances and yet be distinctly separated.

Temperatures at calculated fishing depths at stations where subsurface yellowfin were taken in the northwestern Atlantic were comparable to temperatures of the surface water at positions in the Pacific where surface-dwelling yellowfin were taken.

Shark damage was light. A higher percentage of yellowfin (to 20.6 percent) than bluefin (to 12.5 percent) was attacked at any one exploratory station. Whitetip sharks appear to be responsible for a large share of shark damage to tunas in the western Atlantic.

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GULF OF MEXICO COMMERCIAL SHRIMP POPULATIONS—TRENDS AND CHARACTERISTICS, 1956–59

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Shrimp populations inhabiting shallow coastal waters of the Gulf of Mexico support intensive and valuable fisheries. Fluctuating about a level of 200 million pounds and trending very slightly upward, annual yields over the past decade (1950–59) have risen steadily in value and generally resulted in increased gross receipts for Gulf fishermen and processors. If ex-vessel sales of landings indicate the relative worth of fish or shellfish supplies, then Gulf of Mexico shrimp stocks now rank, collectively, as the most valuable of North American commercial fishery resources.

The close of the decade saw, however, an adverse departure from the value trend established during the preceding 9 years. In 1959, a 22-percent drop in value despite a moderate increase in yield created economic stress throughout much of the industry. Sharply rising imports are generally credited with having fostered this plight. The situation brightened somewhat in 1960 when the yield rose still higher and its value jumped 15 percent.

Notwithstanding the effects of expanding imports on the utilization of domestic supplies, development of management programs for shrimp stocks in United States coastal waters persists as a major objective. Such programs would so regulate fishing that maximum yields consistent with population stability are realized on a continuing basis.[1] Preliminary studies which establish how populations react to varying degrees of exploitation and, at the same time, to a variable environment, necessarily constitute the framework supporting any management program. These studies and, subsequently, the methods used to prescribe optimum fishing rates and predict yields, require detailed statistics of past and current fishing operations.

Acknowledging this need, the Bureau of Commercial Fisheries initiated in 1956 a continuing survey of commercial shrimping activities in the Gulf of Mexico. On the one hand, this survey provides the fishing industry with up-to-the-minute information on trends in shrimp production and marketing of shrimp products; on the other hand, it furnishes data needed to assess the shrimp resource itself and, ultimately, to formulate a resource management program. The following report describes the present survey, reviews trends in annual shrimp yields, attempts an appraisal of commercial shrimp populations employing commercial statistics, and suggests where improvements would enhance the survey's usefulness.

THE GULF OF MEXICO SHRIMP FISHERY

SPECIES EXPLOITED

A half dozen or so members of the family Penaeidae (Crustacea: Decapoda) support the extensive Gulf of Mexico shrimp fishery. Only three, however, contribute significantly to the overall yield. The top-ranked species include the brown shrimp, *Penaeus azteeus* Ives; pink shrimp, *P. duorarum* Burkenroad; and white shrimp, *P. setiferus* (Linnaeus). Lesser forms in descending order of importance are the seabob, *Xiphopeneus kröyeri* (Heller); *P. brasiliensis* Latreille; *P. sehmitti* Burkenroad; and *Trachypeneus* spp. Of these less important shrimps, only the seabob enjoys specific commercial status although it has never contributed more than two percent to the total shrimp production in any one year. The remaining species are frequently taken in small

[1] Changing economy and consumer habits represent important but uncontrollable variables which may preclude attainment of "maximum sustained yields."

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amounts together with brown, pink, or white shrimp, but due to difficulty in distinguishing them from the latter species, are never differentiated by the fishing industry.

Species having potential commercial value include the royal red shrimp, *Hymenopenaeus robustus* Smith, a deep-water species, and the rock shrimps, genus *Sicyonia*, particularly *S. brevirostris* Stimpson, which frequently attains high densities in many areas.

This report treats exclusively the larger, more abundant varieties, namely, the brown, pink, and white shrimp. These are sought on the continental shelf and in contiguous inshore waters from the Florida Keys counterclockwise around the Gulf to the Yucatan Peninsula. Coastal, bathymetric, and seasonal distribution depends upon the species and, to some extent, the general locale. Although all three species occur throughout the Gulf, brown and white shrimp are most abundant along the northern and western coasts, whereas pink shrimp tend to concentrate to the south and east. A major task now confronting biologists is determining whether primary shrimp stocks are homogeneous over their ranges, or whether they comprise discrete subpopulations overlapping in space, time, or both.

The question of population definition is prompted in part by the unique life history of common penaeid shrimps. In general, eggs are fertilized and spawned in the oceanic habitat of the parent shrimp. After a very short incubation period, a small larva or nauplius emerges. Rapid growth accompanied by gross morphological changes ensues, the larva, now a component of the zooplankton, being quickly carried shoreward into broad and shallow estuaries. Transformation to adult likeness and habits occurs somewhat before or as the larva enters inshore waters. Here the shrimp, now a postlarva or juvenile, maintains rapid growth for the next 2 or 3 months. As maturation approaches, it departs from the "nursery" grounds, returning to the parental offshore habitat where its life cycle is completed. The average life span of the more important penaeids is thought to approximate 18 months although there are indications that many female shrimp continue to breed to a more advanced age, tending to make this estimate somewhat low. Pink shrimp captured as large and mature adults have been maintained in aquaria at the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex., for periods exceeding 1 year.

In reconsidering the problem of stock homogeneity, questions arise concerning the relationship between offshore aggregations and the utilization of inshore waters by their progeny. Are there discrete offshore populations that can be consistently defined in terms of specific inshore waters which nurture their offspring? That is, do individual shrimp, after their sojourn in specific inshore waters, return to reproduce in their natal offshore areas; or do most juveniles migrate coastally to other suitable offshore habitat, their progeny, in turn, being nurtured in inshore waters adjacent thereto? Or is there a more or less random interplay between subgroups making up a given stock and the inshore areas their developing progeny occupy, such relationship being tempered to a large degree by varying oceanographic conditions? The fact that mortality in inshore waters is being increasingly compounded by artificial factors, especially by intensified harvest of subadult shrimp, dictates the need for a better understanding of each stock's spatial relationships.

TYPES OF FISHERIES

Each of the common Gulf shrimps is subject to utilization over a broad spectrum of life history stages. Large and small shrimp are utilized for food while the small ones are also important as sport fishing bait. In practically all inshore and offshore waters, commercial and noncommercial fisheries heavily exploit shrimp ranging from small juveniles to the largest adults. The degree to which activities of either interest prevail in a particular area depends largely upon local statutes.

Some States, for example, permit extensive commercial and noncommercial harvesting of small shrimp for human consumption, whereas others stringently enforce closed-season and minimum-size laws. Development of markets made possible by machinery that permits economical processing of small-size ("cocktail") shrimp has stimulated demands for this product. In inshore waters where size laws restrict commercial harvest of immature shrimp for table use, bait shrimp fisheries are now firmly established. These have exhibited such phenomenal growth in recent years that in some areas their collective income frequently exceeds that of the adjacent offshore fishery.

FIGURE 1.—Typical Gulf coast "inshore" shrimp trawler. (Such vessels are in the 30-ft. class, are single-rigged, and have a very shallow draft. This particular vessel has been adapted to a commercial bait-shrimp fishing operation.)

Distinct subunits of the Gulf of Mexico shrimp fishery may thus be defined as follows:

(1) Noncommercial fishery—composed of an untold number of sport fishermen taking mostly immature shrimp for personal use from shallow coastal waters. Fishing gear consists mainly of small otter trawls pulled with outboard-powered craft.

(2) Commercial bait fishery—comprising a fairly large number of professional fishermen taking immature shrimp, almost exclusively in inshore waters, solely for the purpose of supplying bait (live and dead) to a growing population of anglers. Except for the craft, which are inboard-powered and slightly larger, the gear is similar to that described for the noncommercial fishery (Inglis and Chin, 1959).

(3) Commercial fishery—representing the core of the Gulf shrimp industry and composed of a large number of professional fishermen who traditionally seek (1) the larger, mature shrimp inhabiting all coastal offshore waters and (2) small, immature shrimp in certain inshore waters. Except for a very small amount of processing waste which is ground into meal, all of this fishery's harvest is destined for human consumption, the larger shrimp being processed for sale in a fresh or frozen condition, the smaller shrimp being dried or canned.

CHARACTERISTICS OF COMMERCIAL SHRIMP FLEET

Trawlers (fig. 1) of very distinctive design and similar construction comprise a large and highly mobile shrimp fleet. Practically all units par-

FIGURE 2.—Modern Gulf of Mexico "offshore" shrimp trawler. (This vessel was built in 1958, is 57 ft. long, has a capacity of 55 gross tons, a 150-horsepower engine, and is double-rigged.)

ticipating in inshore commercial fisheries are small, shallow-draft, low-powered boats of less than 5 tons net capacity. Most recent estimates place their number between three and four thousand.

Although shallow-draft like their inshore counterparts, shrimp trawlers (fig. 2) plying offshore waters are more sturdily constructed, have greater internal capacity, and are fitted with correspondingly larger power plants. The average sea-going trawler, qualified by an indication of slight increase in size during the period 1956–59, has a register length of about 57 feet, an internal capacity of 50 gross tons, and a power plant rated at 160 horsepower. Significantly, such specifications vary within rather narrow limits for a high proportion of the United States offshore fleet, whose size is estimated at between four and five thousand vessels.

Gulf shrimp trawlers (figs. 2, 3, 4) may be equipped with only the most essential and simplest of navigational devices. Smaller vessels (shorter than 45 feet) ordinarily possess no electronic aids, but many larger craft are fitted with radiotelephones, fathometers, automatic pilots, and radio navigation equipment. Radar, loran, and fish-finding devices will be found only on the largest trawlers.

Following a period of transition (1955–57), trawler rigging throughout the offshore fleet is now quite uniform. Whereas every vessel prior to 1956 was rigged to pull a single large trawl

from a boom located amidship and projecting aft, most offshore trawlers are currently equipped to tow two smaller trawls from booms projecting laterally. Today, the greatest number of single-rigged vessels will be found in the inshore fleet; the capacity to pull two trawls being more or less restricted to larger vessels. Practically all seagoing trawlers constructed since 1958 are double rigged.

Among offshore fishermen there is unanimity of opinion that two sets of small gear are generally easier to handle than a single large gear. Although reducing vessel maneuverability to some extent, they increase speed and range of fishing operations, and lend stability to the vessel when trawling. Some disagreement prevails, however, as to the relative catching ability of two small trawls contrasted to that of one large trawl. It would appear that in some circumstances, disadvantages inherent in one arrangement might offset advantages in the other, resulting in a comparable efficiency from a production standpoint. Knake, Murdock, and Cating (1958) give a comprehensive review of double-rig design and operation.

For the most part, Gulf of Mexico shrimp trawls are quite uniform in shape and dimension. Single- and double-rig trawls are usually "flat" in design, "balloon" types being in the minority. In offshore trawling gear, cod-end mesh dimensions are more or less fixed at 2 or 2¼ inches stretch measure although shrinkage may reduce the average mesh size of individual nets to as

FIGURE 3.—Gulf shrimp trawler of earlier design used in nearshore and inshore fishing operations. (This vessel was constructed in 1943, is in the 40-ft. class, and is single-rigged.)

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FIGURE 4.—Portion of shrimp fleet operating out of Galveston, Texas. (Both inshore and offshore, single-rig and double-rig trawlers are pictured.)

little as 1½ inches. Mesh size in inshore trawls varies little from 1½ to 1⅝ inches. Thread sizes range from 48 to 36 or less in the cod end and from 18 to 12 in the body and wings. Widths of nets along the lead line vary as the size of the vessel but most single-rig vessels fish 90- to 110-foot "flat" or 60- to 90-foot "balloon" nets, and most double-rig vessels fish 40- to 45-foot "flat" nets. In addition, almost every shrimp trawler is fitted with a small (10-foot) searching or "try" net that is towed from a stern davit. At least one innovation at the lead line, the so-called "tickler" chain, has become a standard net accessory. A new one, consisting of wooden discs loosely strung along the lead line, is said to increase net efficiency and greatly reduce gear losses on bad bottom. All nets are fished by means of two otter doors, to each of which a net wing is attached directly. The doors, in turn, are hung on a bridle which joins a single towing warp just forward of the net. A few fishermen are presently experimenting in offshore waters with modified beam trawls, several designs of which have met with success in the inshore bait shrimp fishery.

FISHING OPERATIONS

Length of fishing trip from departure to first landing ranges, in accordance with distance to the shrimping grounds, from 1 to more than 50 days. Whereas most trips along the upper Gulf coast are

ordinarily of 1 to 5 days' duration, trips from United States ports to the distant Campeche grounds occasionally cover a 7-week period. In the latter situation, vessels may transship their catches on others periodically departing for home port and then continue to fish until they, too, leave the fishing grounds at the end of the period indicated. Depending on the species sought, only a relatively small proportion of the time away from port may be spent in actual fishing.

Routine operating procedure is to fish the main net or nets for 1½- to 5-hour periods depending on the density of shrimp. When shrimp exhibit patchy distribution and are scarce, the "try" net is fished continuously for 20- or 30-minute periods until its catch indicates that profitable quantities are available. Searching may frequently extend over as much as 5 days before the main nets are lowered into paying concentrations of market-size shrimp.

Most offshore fishing is at night, reflecting nocturnal activity of brown and pink shrimp which greatly increases their availability. An average night's fishing for these species covers about 10 hours during which time the nets are hauled two to five times, the mean being about three. White shrimp are generally fished during daylight hours, though in certain seasons they may be taken at night along with brown shrimp.

Catches are sorted and iced immediately or soon after removal from the net. If individual shrimp are large and not too numerous, they are beheaded prior to icing. In all other instances, heads remain intact until final processing ashore (fig. 5). Discards of undersized shrimp may be substantial at certain seasons, but accurate measures of their magnitude for any season or area have never been obtained.

More specific details of shrimp fishing and processing operations may be found in U.S. Fish and Wildlife Service (1958).

COMMERCIAL FISHERY STATISTICS

Accurate statistics of trawling operations and shrimp production in the Gulf of Mexico were not maintained prior to 1956. In that year a Gulf-wide statistical survey was inaugurated to provide a continuous flow of data that would facilitate studies of fishery economy and biology. It has since functioned with no major changes.

From the outset, however, survey resources permitted full statistical coverage only of that fishery centering on the commercial utilization of shrimp for human consumption. Operations and production in noncommercial and commercial bait fisheries have gone largely unrecorded. As a consequence, available statistics give an incomplete picture of total shrimp harvest in the Gulf coast area, and allow appraisal of only those portions of populations supporting what was defined earlier as the "commercial" fishery.

In studies using data obtained from sources such as the present survey, a review of survey design and techniques helps to place in proper perspective interpretations of analyses to which resulting data may be subjected.

DISTRIBUTION OF SURVEY PERSONNEL

Sixteen "statistical" or "port" agents record the day-to-day operations and production of the United States commercial shrimp fleet. Strategically located at landing ports around the Gulf—four in Florida, one each in Alabama and Mississippi, and five each in Louisiana and Texas—they canvass fishermen and processors for detailed information on location and amount of fishing, volume and composition of shrimp landings, and current marketing conditions, relaying it after necessary adjustment to Washington, D.C., for final processing. This consists of assembling the data on a monthly basis and publishing them in tables entitled "Gulf Coast Shrimp Catch by Area, Depth, Variety, and Size."

IDENTIFICATION OF FISHING GROUNDS

To facilitate geographical assignment of commercial trawling effort and hence classification of shrimp landings as to origin, the continental shelf of the Gulf of Mexico has been subdivided coastwise into 40 statistical subareas (fig. 6). Numbered counterclockwise beginning off the Florida Keys, these have been further subdivided from the shoreline to 45 fathoms into three depth zones, and grouped into eight coastal areas. Bottom areas for each statistical unit are given in table 1.

DISTRIBUTION AND AMOUNT OF FISHING EFFORT

One of two important variables involved in measuring demersal populations is the time spent trawling, referred to herein as fishing effort. It was and continues to be estimated by means of

equivocal sampling and projection techniques. A system of interviewing trawler captains provides the basis for acquiring this and other information.

The number of trawler captains each port agent is able to interview, per week, may vary from none to 25 or more depending on his other duties, the likelihood of contacting captains during the hours he can set aside for this purpose, and the cooperation of the captains themselves. As time and circumstances permit, landing sites are visited and information concerning operations of their trawlers is solicited from those captains who are on hand. Data on areas and depths fished as well as time spent trawling at each fishing position are entered on a "Report of Interview." Also sought are the captain's observations of the number of other craft that operated in the vicinity of his trawler during its most recent trip.

It is then assumed: (1) that all trawlers landing at a given port operated in the same general area(s) and at the same depths as those for which data were secured by interview, and (2) that for all craft, a simple linear relationship obtains between amount of trawling time and size of corresponding

FIGURE 5.—Unloading catch of whole shrimp at a modern Gulf coast processing plant. Hopper (at far end of conveyor) is lowered into vessel's hold and facilitates unloading. (Ice is removed by means of bath situated midway along the conveyor which carries the shrimp to the processing facility.)

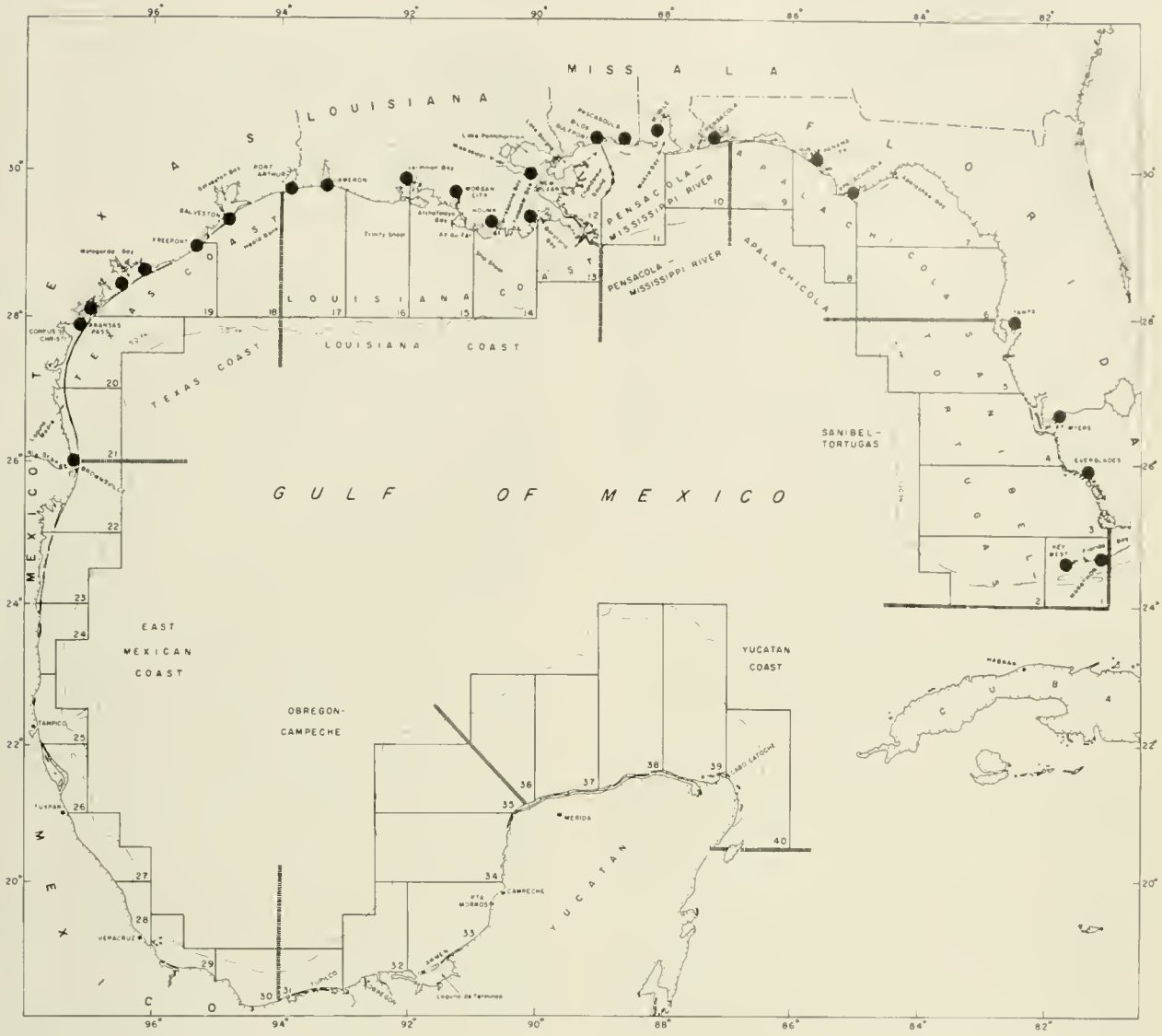

FIGURE 6.—System for coding origin of shrimp landings and position of commercial shrimping operations in the Gulf of Mexico. Shaded circles indicate principal landing ports.

catch. Fishing positions during concurrent trips of trawlers whose captains are not interviewed are projected and coded accordingly. The quantity of effort expended is calculated by merely dividing their known catches by a projection factor derived from catch-effort ratios of the vessels actually sampled for operating data. Effort is recorded to the nearest tenth in terms of days' trawling time or, more precisely, the total number of hours trawled divided by 24. "Day" then does not refer to a calendar day but merely represents a coding device.

Biases affecting the usefulness of effort data secured by this technique will be discussed in a later section, but two shortcomings should be pointed out here. The first concerns estimating nonproductive fishing effort. During certain seasons considerable amounts of searching ("try-netting") and fishing time are expended with negligible results. Under the present system, such activity goes unaccounted for since effort is estimated for and assigned only to vessel-trips for which a shrimp sale is recorded. Exclusion of this nonrewarded effort obviously leads to under-

TABLE 1.—*Projected bottom area off the Gulf of Mexico coast from Marathon, Florida, to Cabo Catoche, Yucatan* [1]

[Square nautical miles]

Coastal area and subarea [2]	Depth (fm.)			
	0–10	10–20	20–45	Total
Sanibel-Tortugas:				
1	1,410	45	60	1,515
2	650	1,045	1,355	3,050
3	2,400	2,080	3,120	7,600
4	1,230	1,665	2,575	5,470
5	950	1,420	2,755	5,125
Subtotal	6,640	6,255	9,865	22,760
Apalachicola:				
6	1,750	2,825	2,050	6,625
7	2,860	1,915	80	4,855
8	430	1,485	840	2,755
9	60	765	790	1,615
Subtotal	5,100	6,990	3,760	15,850
Pensacola-Mississippi River:				
10	330	1,315	805	2,450
11	895	950	1,030	2,875
12	185			185
Subtotal	1,410	2,265	1,835	5,510
Louisiana Coast:				
13	420	220	475	1,115
14	990	680	970	2,640
15	1,810	760	1,225	3,795
16	1,580	1,590	1,610	4,780
17	1,950	1,800	1,660	5,410
Subtotal	6,750	5,050	5,940	17,740
Texas Coast:				
18	1,770	1,370	1,660	4,800
19	885	1,815	825	3,525
20	360	965	1,710	3,035
21	285	610	1,350	2,245
Subtotal	3,300	4,760	5,545	13,605
East Mexican Coast:				
22	395	660	1,245	2,300
23	280	440	1,055	1,775
24	320	225	615	1,160
25	270	400	805	1,475
26	270	330	525	1,125
27	160	230	480	870
28	145	160	350	655
29	125	170	390	685
30	110	230	540	880
Subtotal	2,075	2,845	6,005	10,925
Obregon-Campeche:				
31	130	605	385	1,120
32	565	935	655	2,155
33	2,485	1,375	835	4,695
34	1,935	1,810	2,230	5,975
35	450	1,710	5,560	7,720
Subtotal	5,565	6,435	9,665	21,665
Yucatan Coast:				
36	235	530	2,055	2,820
37	835	1,460	2,765	5,060
38	920	1,260	4,625	6,805
39	965	1,140	3,775	5,880
40	320	585	875	1,780
Subtotal	3,275	4,975	14,095	22,345
Gulf of Mexico	34,115	39,575	56,710	130,400

[1] Source: Charts issued by U.S. Coast and Geodetic Survey and U.S. Navy Hydrographic Office. Untrawlable bottom not delineated.
[2] Refer to figure 1.

estimates of individual vessel and fleet trawling time. Secondly, the assumption that all vessels operating out of or landing at a particular port fish in close proximity may not always be valid. It is acknowledged, however, that portions of the fleet fishing a specific locale usually tend to aggregate on shrimp concentrations occurring there. The question of how fishing positions and effort are assigned to vessels operating in periods during which interview data cannot be obtained remains unreconciled.

LANDINGS

Equivalent in importance to the variable, "effort," is the corresponding variable, "catch." The present statistical survey attempts to account for all commercial shrimp landings through a daily or weekly canvass of processing plants. From dealers' receipts, port agents transcribe the details of landings for each vessel-trip on a "Shrimp Schedule" form. An estimated 97–100 percent of all Gulf shrimp landings are so reported each year. Contrasted to other types gathered by the survey, data of commercial landings may be considered complete and, in addition, quite precise, since they are factors in business transactions. Unfortunately, recorded landings may not always represent the amount of shrimp actually caught. This is usually attributable to the periodically widespread practice of discarding at sea small or otherwise undesirable shrimp.

Origin

Each landing is coded according to its known or "estimated" origin in the same manner as that described earlier for coding a vessel's fishing position.

Prorating landings by depth of capture is one procedure here that could lead to misrepresentation of tabulated data. If a captain states that he trawled in several depth zones but cannot specify how his trawling time and catches were apportioned among them, his total effort and corresponding catch will be coded, respectively, as having been expended in and taken from the zone of greatest depth fished. Accumulations of catch-by-depth data obtained by interview for a very small proportion of the commercial shrimp fleet, and by projection therefrom for the greater part of the fleet, have limited usefulness in depth distribution studies of commercial species. Some will be falsely described as having been available in larger quantities over a greater depth range than they actually were.

Species Composition

Along much of the Gulf coast, processors distinguish between commercial varieties commonly occurring together by assigning slightly different ex-vessel prices to each. A breakdown by species for each landing is thus obtained automatically when transcribing landing data from dealers' records.

In some areas, however, closely related species are not differentiated by price. Here mixed landings of two species may be described as entirely composed of one or the other, resulting in distorted catch figures for both. Examples of areas in which this situation periodically exists are southwest Florida and Texas. In the former area, *Trachypeneus* spp., which have little commercial value because of their small size, frequently enter pink shrimp landings in small amounts. In contrast, pink shrimp often dominate spring landings at Freeport, Aransas Pass, and perhaps other Texas ports, being purchased and entering dealers' records as brown shrimp. The degree to which past landing data from these and other areas are so biased has not been determined. An attempt is being made to rectify this problem by establishing a Gulf-wide catch-sampling program.

No evidence of preference on the part of the commercial fleet for a particular species (in situations where more than one were equally available) was detected in the present study.

Size Composition

Ex-vessel sales are prorated on the basis of each landing's size composition as well as its species composition, with larger shrimp bringing higher prices. Landings are thus recorded according to the sizes purchased from the fisherman, the breakdown being carried through to final tabulation.

Although such a practice might appear to obviate the need for sampling shrimp landings to secure a picture of population size or age structure, closer scrutiny raises some doubt as to the commercial data's usefulness for this purpose. Comparability of size composition data from different Gulf areas may be suspect due to the following biases of unknown degree: (1) varying minimum-size laws; (2) differential dealer and gear selectivity; (3) changing prices; and (4) different grading methods. Further discussion of these factors will be deferred to a later section.

CONVERSION FACTORS

As a convenience to commercial interests, shrimp landing statistics are compiled in terms of "tail" or headless weight. In keeping with the ecological convention of maintaining unit correspondence between yield and biomass, all landings reported herein have been converted to whole or "heads-on" weight. This was accomplished by applying the factor 1.68 to catch data published for each common species.

Unfortunately, the statistical reliability of this factor has not been established. Moreover, current studies indicate that among commercial Penaeidae, the factors relating headless to whole weight vary widely between species and to a lesser extent between sexes and from season to season within species, and are measurably less than formerly believed. Ratios between total and tail weight for the brown, pink, and white shrimp and seabob (sexes combined over all seasons) have been found to deviate only slightly (coeficients of variation are 3 percent or less) from 1.61, 1.60, 1.54, and 1.53, respectively. These represent significant departures from the traditional 1.68.

Conversion from headless to whole weight would not constitute a problem if all shrimp were landed and weighed heads-on. Published data could be restored to their original and desired state by simply applying the reciprocal of whatever factor was used to convert them to heads-off units. But commercial shrimp are not handled in uniform fashion around the Gulf. Many are landed heads-on, many heads-off, the former being converted to heads-off units immediately upon being landed. The degree to which either practice is followed in each area is unknown and, consequently, so is the relative accuracy of adjusted landings data. If landings heads-on predominate, the inaccuracy of data converted using a generalized factor will be minimal. But if heads-off landings are the rule, data converted using the same factor (1.68) will not reflect true catch (heads-on) weights for all species. In either case, landing data will not be comparable from area to area and, in some instances, from port to port within an area.

Further complications arise if conversion of catch-by-size data is desired. All such data are recorded in terms of number of headless shrimp

per pound, with eight or nine "size-count" categories in common use along the Gulf coast. Notwithstanding the possible influence of biases noted in the foregoing section, any conversion of landings within size-count categories would necessitate a corresponding change in the size-count scale. Size-count notation for headless and corresponding whole shrimp is given in table 2.

TABLE 2.—*Numbers per pound of headless and corresponding whole shrimp. A constant ratio of 1.68 between total and "tail" weight is assumed*

Number of headless shrimp per pound	Weight per "tail" (oz.)	Weight per whole shrimp (oz.)	Approximate number of whole shrimp per pound
10	1.60	2.69	6
12	1.33	2.23	7
15	1.07	1.80	9
18	.80	1.50	11
20	.80	1.34	12
25	.64	1.08	15
30	.53	.89	18
35	.46	.77	21
40	.40	.67	24
50	.32	.54	30
60	.27	.45	35
68	.24	.40	40
75	.21	.35	45

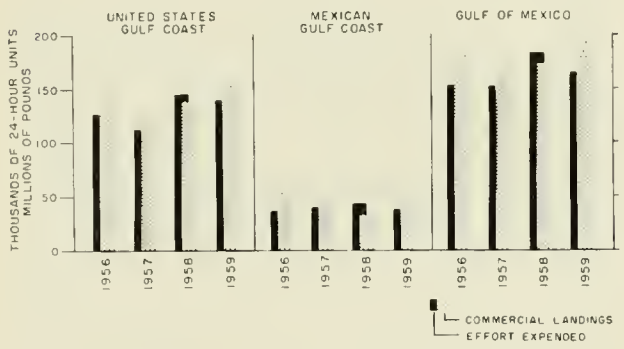

FIGURE 7.—Effort expenditure and total commercial landings by the United States shrimp fleet, Gulf of Mexico, 1956–59.

FISHING EFFORT AND TOTAL SHRIMP YIELD, 1956–59

For the years 1956–59, annual fishing effort on Gulf of Mexico shrimp grounds deviated only slightly from an average of 169 thousand days (fig. 7, table 3). Corresponding shrimp harvests exhibited no startling trend, fluctuating between 167 and 193 million pounds with a maximum deviation from the 4-year mean of only 8 percent. Effort expended in and catches from foreign Gulf waters averaged 23 and 22 percent, respectively, of overall Gulf of Mexico totals (tables 3 and 4).

Another look at overall effort and catch data after they are separated into their spatial and

TABLE 3.—*Fishing effort expended by United States commercial shrimp trawlers in the Gulf of Mexico, 1956–59* [1]

[24-hour units]

Coastal area	Year			
	1956	1957	1958	1959
Sanibel-Tortugas:				
Inshore	0	0	0	0
Offshore	17,519.0	17,335.9	20,689.9	17,097.9
Total	17,519.0	17,335.9	20,689. 9	17,097.9
Apalachicola:				
Inshore	1,692.6	2,601.4	2,564.3	1,799.6
Offshore	2,262.5	1,739.3	1,686.5	1,382.0
Total	3,955.1	4,340.7	4,250.8	3,181.6
Pensacola-Mississippi River:				
Inshore	12,780.8	12,669.8	12,530.3	15,547.2
Offshore	12,871.6	10,260.6	6,941.3	9,654.8
Total	25,652.4	22,930.4	19,471.6	25,202.0
Louisiana Coast				
Inshore	15,700.6	13,112.4	20,209.4	21,405.8
Offshore	30,225.4	18,103.0	32,554.3	32,368.9
Total	45,926.0	31,215.4	52,763.7	53,774.7
Texas Coast:				
Inshore	2,267.7	3,927.0	4,726.7	4,157.7
Offshore	31,801.7	33,699.3	41,859.1	35,057.7
Total	34,069.4	37,626.3	46,585.8	39,215.4
United States Gulf Coast:				
Inshore	32,441.7	32,310.6	40,030.7	42,910.3
Offshore	94,680.2	81,138.1	103,731.1	95,561.3
Total	127,121.9	113,448.7	143,761.8	138,471.6
East Mexican Coast:				
Inshore	0	0	0	0
Offshore	14,375.4	17,267.0	24,191.6	17,611.3
Total	14,375.4	17,267.0	24,191.6	17,611.3
Ohregon-Campeche:				
Inshore	0	0	0	0
Offshore	22,235.8	21,490.7	16,899.2	19,709.1
Total	22,235.8	21,490.7	16,899.2	19,709.1
Mexican Gulf Coast:				
Inshore	0	0	0	0
Offshore	36,611.2	38,757.7	41,090.8	37,320.4
Total	36,611.2	38,757.7	41,090.8	37,320.4
Total Gulf of Mexico:				
Inshore	32,441.7	32,310.6	40,030.7	42,910.3
Offshore	131,291.4	119,895.8	144,821.9	132,881.7
Total	163,733.1	152,206.4	184,852.6	175,792.0

[1] Breakdown of fishing effort according to amounts expended seasonally in inshore and offshore waters is made in appendix table 1.

TABLE 4.—*Commercial shrimp landings by United States trawlers, Gulf of Mexico, 1956–59* [1]

[Thousands of pounds]

Coastal area and species	Year			
	1956	1957	1958	1959
Sanibel–Tortugas:				
Brown	0	0	1.3	0.7
Pink	21,392.6	16,688.8	24,698.8	13,914.7
White	0	0	0	2.0
Seabobs	0	0	0	0
Total	21,392.6	16,688.8	24,700.1	13,917.4
Apalachicola:				
Brown	285.0	560.3	992.2	1,240.5
Pink	1,337.7	898.0	2,500.8	11.1
White	852.3	1,281.6	1,358.0	582.9
Seabobs	79.7	348.9	16.7	229.8
Total	2,554.7	3,088.8	4,867.7	2,064.3
Pensacola–Mississippi River:				
Brown	16,395.5	15,284.7	8,793.4	19,103.8
Pink	799.9	881.9	194.4	281.1
White	6,984.5	3,181.9	4,967.9	7,513.4
Seabobs	4.7	0	0.8	16.3
Total	24,184.6	19,348.5	13,956.5	26,914.6
Louisiana Coast:				
Brown	21,245.4	18,572.8	16,424.9	27,260.5
Pink	2.6	0	18.9	10.2
White	28,741.7	10,526.4	23,971.4	24,066.4
Seabobs	1,521.3	742.7	1,826.3	3,708.1
Total	51,511.0	29,842.3	42,241.5	55,045.2
Texas Coast:				
Brown	37,318.9	49,008.0	40,477.0	49,564.5
Pink	62.4	7.0	126.3	15.9
White	4,410.4	3,568.9	11,475.0	8,259.1
Seabobs	0	0.2	2.2	0
Total	41,791.7	52,584.1	52,080.5	57,839.5
United States Gulf Coast:				
Brown	75,244.8	83,425.8	66,688.8	97,170.0
Pink	23,595.2	18,475.7	27,539.2	14,233.0
White	40,988.9	18,558.8	41,772.3	40,423.8
Seabobs	1,605.7	1,091.8	1,846.0	3,954.2
Total	141,434.6	121,552.1	137,846.3	155,781.0
East Mexican Coast:				
Brown	16,374.0	23,760.2	18,423.0	18,511.0
Pink	4.7	0	10.1	16.0
White	48.3	2.5	259.7	241.6
Seabobs	0	0	0	0
Total	16,427.0	23,762.7	18,692.8	18,768.6
Obregon–Campeche:				
Brown	751.1	398.2	815.5	1,560.6
Pink	24,541.1	21,281.0	13,430.3	16,402.6
White	19.6	86.4	358.6	202.3
Seabobs	0	0	0	0
Total	25,311.8	21,765.6	14,604.4	18,165.5
Mexican Gulf Coast:				
Brown	17,125.1	24,158.4	19,238.5	20,071.6
Pink	24,545.8	21,281.0	13,440.4	16,418.6
White	67.9	88.9	618.3	443.9
Seabobs	0	0	0	0
Total	41,738.8	45,528.3	33,297.2	36,934.1
Total Gulf of Mexico:				
Brown	92,369.9	107,584.2	85,927.3	117,241.6
Pink	48,141.0	39,756.7	40,979.6	30,651.6
White	41,056.8	18,647.7	42,390.6	40,867.7
Seabobs	1,605.7	1,091.8	1,846.0	3,954.2
Total	183,173.4	167,080.4	171,143.5	192,715.1

[1] Breakdown of landings according to amounts taken seasonally from inshore and offshore waters is made in appendix tables 2–4.

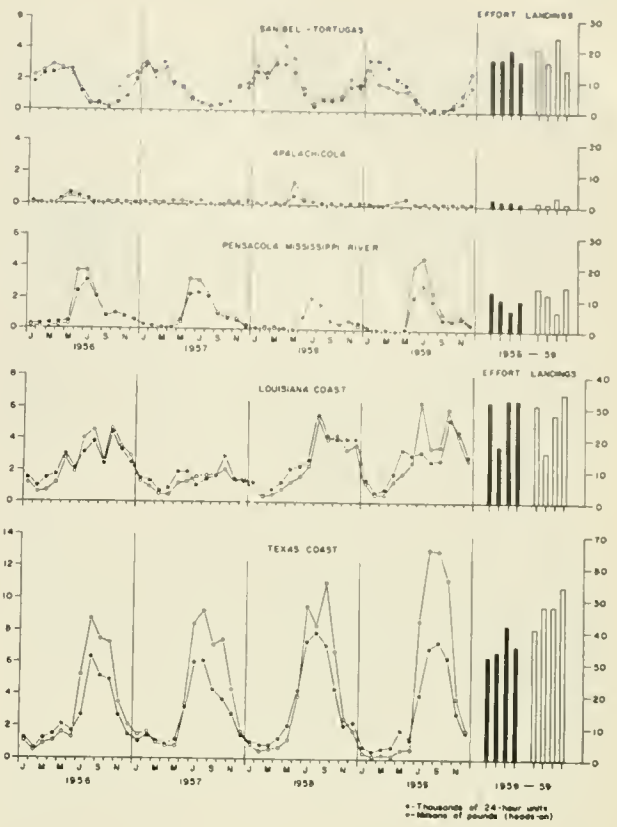

FIGURE 8.—Effort expenditure and commercial shrimp landings by United States trawlers operating off the United States Gulf coast, 1956–59.

temporal components reveals, however, significant fluctuations and trends within coastal units. For instance, effort and total yield exhibited distinct seasonal patterns in the Sanibel-Tortugas, Pensacola-Mississippi River, Louisiana Coast, and Texas Coast offshore areas. Total landings periodically dropped to unfavorable lows in the Sanibel-Tortugas (1957, 1959), Pensacola-Mississippi River (1958), and Louisiana Coast (1957) areas (fig. 8); established a significant upward trend in the Texas Coast area; and declined appreciably over the 4-year period in the Obregon-Campeche area. Annual effort expenditure and yield were comparatively stable in the Apalachicola area (figs. 8 and 9). Waters off the Texas and Louisiana coasts ranked, in that order, as top shrimp producers.

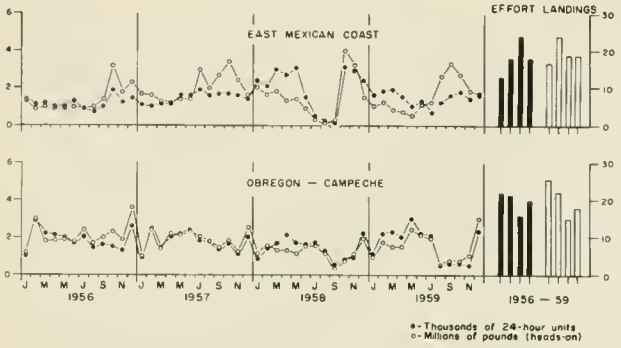

FIGURE 9.—Effort expenditure and commercial shrimp landings by United States trawlers operating off the Mexican Gulf coast, 1956–59.

The sinuous nature of monthly yield curves indicates to some extent the seasonal reproductive patterns typical of the short-lived penaeid shrimps. High correspondence between curves of effort and yield generally reflects the techniques used to estimate the former from the latter.

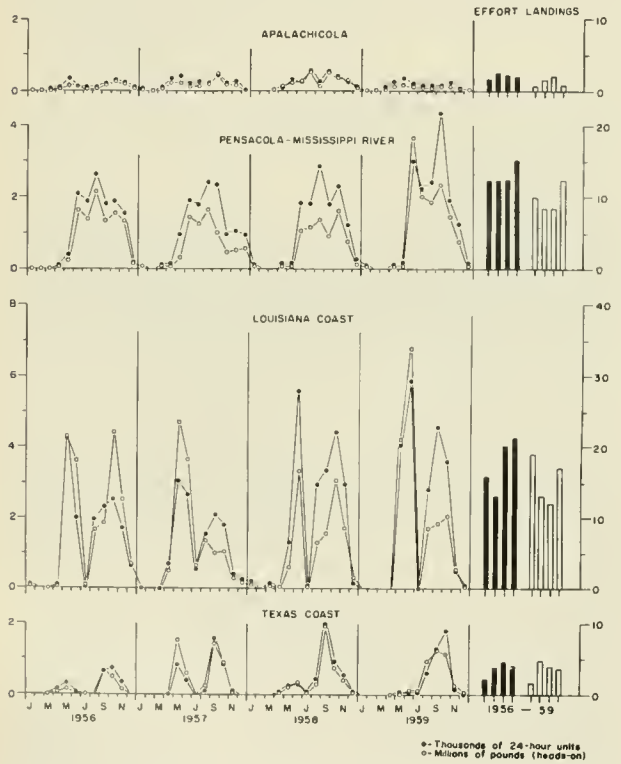

FIGURE 10.—Effort expended in and commercial shrimp landings from inshore waters along the United States Gulf coast, 1956–59.

Exploitation of "table" shrimp by the United States fleet in inshore (estuarine) waters bordering the Gulf of Mexico is restricted to northern coastal areas (table 3). Practically all landings from such waters consist of small shrimp, some of which are dried, but most of which are now economically machine-processed for canning.

Of the four northern Gulf coast areas designated in this report, the Louisiana Coast area claims the greatest acreage of inshore waters. This is reflected in its inshore shrimp production which, during 1956–59, annually exceeded that of any other area (fig. 10). Note, however, that while inshore landings from adjacent areas exhibited little tendency toward marked fluctuation, those from the Louisiana marshes did, with adverse lows occurring in 1957 and 1958.

A breakdown of landings by years, coastal area (offshore and inshore waters combined), and species reveals major differences in amounts of the various shrimps taken commercially from each area (table 4). Relative to those of other species belonging to the same taxon and occupying the same range, fluctuations in a particular species population as evidenced by its yield may be masked when dealing with data of composite landings. Obviously, the degree to which fluctuations in each population comprising a multispecies fishery govern overall yield patterns depends largely upon how much the species overlap in occurrence. Attempts to reconcile unusual drops in total yield must therefore take into account variations in the catches of each species contributing to it. Moreover, they must rely on available commercial statistics to depict accurately in space and time, the population size and structure.

METHODS OF POPULATION APPRAISAL

Before attempting to determine how commercial fish and shellfish populations react to exploitation and a varying environment, suitable indicators of population size and composition must be obtained. The capacity of commercial statistics to provide these is wholly contingent upon the nature of the species involved and the mechanics underlying its exploitation.

FISHABLE BIOMASS INDEX

Definition and Theory

Shrimp, being demersal organisms capable of instantaneous but limited vertical and lateral

movement, are highly susceptible to capture by bottom trawls of all types. The average minimum size of shrimp retained by "standard-mesh" [2] trawls sets the lower limit of what is referred to herein as the fishable population. Hence the *fishable biomass* is that fraction (in terms of weight) of a commercial population, which comprises those individuals vulnerable to capture with the gear commonly used by the fishery. Whether or not landing data include everything caught by the gear employed is a matter of vital concern. It is recognized that even though standard-mesh trawls may be used at all times, the minimum size of shrimp *selected* from their catches, not the minimum size *actually caught*, sets the lower limit of that part of the overall population about which corresponding commercial statistics can give any information. The extent to which selection practices prevail varies in unpredictable fashion from area to area and season to season. Departures from the definition of fishable biomass given above can also be attributed to fishing practices wherein standard-mesh gear is employed, but aggregations of shrimp of a specified minimum size are first sought out by trial fishing. Although this circumvents sorting catches predominated by small shrimp, and thereby mitigates the discard problem, the resulting statistics are quite restrictive as to the information they give about the whole population.

Assume now that the geographic range of a given shrimp population is approximately known. If the manner in which commercial trawls are deployed over it during equivalent time increments is also known, an index to the true probability with which a standard unit of the fishable biomass will have been removed can be derived for each increment. A factor proportional to the *average* harvestable biomass is thus obtained when the corresponding (total) commercial catch is divided by this "probability-of-capture" index. The latter has been termed the "effective overall fishing intensity" ($\bar{f}$) by Beverton and Holt (1957) who discuss its theoretical aspects and derivation. For any time interval and population, it is the weighted average of all fishing intensities calculated for each trawling subarea included in the population's range. The fishing intensity in any subarea is simply the ratio between the amount of effort expended therein and the subarea's size. Weighting factors are the subareas' corresponding biomass indices. Since the ratio between catch (in weight) and effective overall fishing intensity is proportional to the fishable biomass, it follows that the fishing intensity is also proportional to the fishing mortality parameter, an important consideration in attempts to evaluate the latter.

To obtain biomass indices directly, Gulland (1955) uses a method almost identical mathematically to that introduced by Beverton and Hold (1957). For a short interval of time, say a month, catch (in weight)-effort ratios are calculated for each subarea within a species range. A weighted average catch-effort ratio is then determined, the sizes of each subarea consitituting the weighting factors. This ratio, the same as that derived above, is theoretically proportional to the size of the population's exploitable fraction, and hence is termed a fishable biomass index. In effect, it is a density estimator in which the effects of uneven distribution of fishing effort are eliminated by a process analogous to stratified sampling.

Error and Bias

Many factors, however, operate to alter the theoretical utility of this index. Some of these, namely error and bias associated with compiling landing and effort data, have already been discussed. Controlling their influence entails refinement of sample projection and data collection techniques. Superimposed on compilation defects, however, are still others which, because of their inconstancy, are very difficult to cope with. Two classes may be readily distinguished.

The first affects the comparability of effort statistics and stems from differences in trawler fleet composition along with nonuniformity of operating conditions. All trawlers are not equally powerful, are not manned by equally efficient crews, and do not operate under identical climatological and sea conditions. For instance, since gear efficiency is directly related to ground speed (up to some optimum point), under conditions of uniform shrimp density, identically powered and rigged vessels operating against the current would normally be expected to make smaller catches per unit time than those operating with it. The writer has observed a low resultant ground speed

[2] The term "standard-mesh" is defined as that size mesh most commonly used in a particular fishery, be it inshore or offshore. Both fisheries are treated separately throughout this report with 1⅝-inch mesh being considered the standard inshore, 2¼-inch mesh the standard offshore. A major requirement is that this average mesh size remain constant.

(water speed minus velocity of opposing surface current) to render forward progress of trawling gear almost negligible. Under the same conditions but traveling in the opposite direction, indications were that too high a resultant ground speed kept the gear off the bottom a high proportion of the time, even at reduced power settings. This was an extreme situation involving operations in deep water (150 fm.) and a very confused sea, but it does serve to illustrate that there is always a "best" combination of factors that results in maximum efficiency for any piece of gear. It would seem quite unlikely that this combination is attained in every fishing operation (see also Dickson, 1961). Also, all other factors being equal, larger trawlers with greater horsepower ratings tend to outfish their lesser counterparts (U.S. Fish and Wildlife Service, 1959). Such factors interacting to varying degree and generating operational biases of unknown magnitude, conceivably play a major role in governing the accuracy of the fishable biomass index.

At least one form of operational bias, that due to differential power of trawlers, has been the subject of detailed study. Gulland (1956) provides a method for its elimination if accurate effort and catch data can be obtained for individual vessels on a per unit space and time basis. As already noted, however, effort statistics used in the present study were projected from sample interview data on the premise that all trawlers are equally efficient. Such treatment automatically nullifies "standardization" of available effort data.

The second class of defects includes miscellaneous error or bias arising from natural factors. For example, patchy distribution of shrimp could result in highly variable catches by individual vessels despite uniform effort, the magnitude of corresponding "sampling error" being such that index precision is greatly diminished. Also, "saturation" of trawls by the species sought as well as by associated fauna, e.g., other invertebrates and fishes, reduces gear efficiency and thereby compounds the inaccuracy of the population density index. Finally, all of a population's fishable biomass may not be available because rough bottom and sundry impediments preclude trawling over portions of its geographic range.

Assumptions

Once the purposes of a statistical survey are clearly defined, an objective should be to minimize the combined effects of sampling error and bias on the estimates being sought. This implies that, in situations such as described here, detailed information on: weather and sea conditions; trawling course with respect to wind and current; water speed; vessel size, horsepower, gear reduction ratio, and screw specifications; fishing gear specifications; incidence of miscellaneous fauna in the catch; etc. should accompany basic effort and catch data, all recorded on a per vessel-trip, per unit space and time basis. Appropriate adjustments would eliminate unwanted effort bias to a substantial degree. Refined catch-effort data would permit a more sophisticated statistical treatment and hence a minimizing of sampling error. Higher quality biomass indices would result.

The condition of available effort data plus the lack of information that would allow adjustment for bias and reduction of error, thwarted attempts to rectify defects in the data used to construct biomass indices. As a consequence, some assumptions regarding the magnitude and effect of error and bias associated with operational and natural factors had to be made. Thus, acknowledged uniformity in size composition of major portions of both inshore and offshore trawler fleets led to the conclusion that bias due to differential efficiency of operating unit was probably not too great. Effects of varying crew ability, climatological and sea conditions, and contagious distribution of shrimp were, within each of the smallest time increments employed, assumed random with zero expectation. And, any shrimp otherwise vulnerable but unavailable because of untrawlable bottom presumably comprised a constant fraction of the total shrimp biomass. Since most interest attached to population trends generated over a 4-year period, an overriding assumption was that the direction and magnitude of all error or bias remained constant for each time interval within that period.

Computation

Calculation of monthly indices for those portions of a population's fishable biomass that occupied offshore areas proceeded according to Gulland's (1956) technique. The seaward limit of each species "commercial" range was arbitrarily set at the 45-fathom contour, this decision was based upon catch statistics (appendix), depth distribution studies (e.g., Burkenroad, 1939), and miscella-

neous observations (e.g., Springer and Bullis, 1956). To simplify calculations, three subsubareas or depth zones were designated for each coastal subarea, viz., 0–10, 11–20, and 21–45 fathoms. Catch and effort totals for each were obtained by combining data from included 5-fathom depth zones. In a few instances where no effort was expended in a particular depth zone, information derived by consolidating data from adjacent zones was assumed indicative of population status in that zone.

To illustrate the mechanics of index computation, let us select for treatment some statistics typical of the Gulf coast shrimp fishery. Table 5 gives published commercial effort and brown shrimp catch figures (June 1958) for each of 12 unequal subsubareas comprising the Texas Coast offshore trawling grounds. If it is assumed that these statistics are reasonably accurate and that the biomass as manifested by the ratio of catch to effort (d_i) was constant within each of the i subsubareas throughout the period indicated, then, from the theory outlined above, the best index of *overall* population biomass is the weighted mean catch-effort ratio for each subsubarea. Hence

$$\sum_i w_i d_i = 0.68 = \text{Fishable Biomass Index}$$

where w_i, the areal weighting factor, is the proportion of the total occupied area represented by the i^{th} subsubarea. The following identity relates, in terms of their notation, the corresponding concepts of Gulland (1955, 1956) and Beverton and Holt (1957):

$$\frac{\sum_i Y_i}{\bar{f}} = \frac{\sum_i Y_i}{\sum_i f_i\left(\frac{Y_i}{f_i}\right)} = \frac{\sum_i Y_i}{\sum_i Y_i} = \sum_i \frac{Y_i}{f_i}$$

$$= \frac{\sum_i a_i \frac{Y_i}{g_i}}{\sum_i a_i} = \frac{\sum_i a_i d_i}{\sum_i a_i} = \sum_i w_i d_i$$

where $f_i = g_i/a_i$ is the fishing intensity in the i^{th} subsubarea; Y_i/f_i is the index of fishable biomass in the i^{th} subsubarea; and the remaining notation is as given in the heading of table 5.

TABLE 5.—*Commercial statistics from the offshore (brown) shrimp fishery in the Texas Coast area, June 1958*

Statistical subarea	Depth subsubarea (fm.) i	Area (sq. naut. miles) a_i	Areal weighting factor w_i	Total effort (24-hr. units) g_i	Total catch (1,000's of lb.) Y_i	Total catch / Total effort d_i
18	0–10	1,770	0.13	246.5	64.6	0.26
	11–20	1,370	.10	731.6	822.8	1.13
	21–45	1,660	.12	6.1	6.2	1.02
19	0–10	885	.06	149.8	38.0	.25
	11–20	1,815	.13	685.5	500.1	.73
	21–45	825	.06	3.6	1.7	.47
20	0–10	360	.03	148.1	140.1	.95
	11–20	965	.07	1,694.5	1,652.1	.98
	21–45	1,710	.13	18.0	10.6	.60
21	0–10	285	.02	6.8	1.2	.18
	11–20	610	.05	284.0	200.9	.71
	21–45	1,350	.10	396.5	236.2	.60
Area totals	....	13,605	1.00	4,371.0	3,674.5	.84

The value obtained, 0.68, may also be referred to as the "catch per unit effective fishing intensity" to distinguish it from the "simple catch per unit fishing effort", 0.84, the value obtained and employed as a population index if, as would have been necessary had effort and catch statistics not been available on a subsubarea basis, the biomass were assumed uniformly distributed throughout the coastal area being studied. Had the latter situation prevailed, an overall population level too high by about 24 percent would have been indicated.

Since commercial fishing effort tends to concentrate in areas of greatest density, the simple catch-effort ratio usually "overestimates" overall population density. Actually, this ratio would constitute as good an index of population size as that between catch and intensity if the effort distribution bias remained constant. This not being the rule, the catch-intensity ratio thereby establishes itself as the more efficient and consistent of the two possible estimators. In cases where there is no alternative but to use the simple catch-effort ratio as a biomass index, a high proportion of its differential between successive time intervals could just as easily be attributed to changes in effort distribution as to real changes in population biomass.

Crude monthly indices of biomass during those stages of population development occurring in inshore waters were secured by calculating the ratio between total commercial catch and total unweighted effort as recorded for such waters. These totals were obtained for each coastal area by summing monthly catch and effort data over specific inshore waters included therein. Such

indices are termed "yields per day's trawling" to distinguish them from their offshore counterparts, "fishable biomass indices."

SIZE-AGE STRUCTURE: FISHABLE BIOMASS

Commercial landings classified according to the sizes of shrimp comprising them afford some insight into fishable biomass age structure only if the landings represent the defined biomass with reasonable accuracy. Any effects of differential bias due to (1) fisherman or gear selectivity; (2) nonuniform distribution of shrimping effort with respect to stratification by age within the fished population; (3) minimum-size restrictions; and (4) varying grading practices must be assumed negligible, or at least constant in time.

Totals for the seven or eight size categories into which commercial shrimp landings are separated give weight frequencies whose modes, it is believed, crudely delineate the age classes, or "*broods*", making up the exploited biomass. The term "brood" is used to define groups of shrimp, each member of which is produced (i.e., spawned and hatched) within a designated interval of time. These intervals are specified as covering periods of heightened spawning activity and extend roughly 1 month on either side of points in time at which modal spawning occurs. Note that modal spawning does not necessarily recur at precisely the same point in successive (corresponding) seasons.

Monthly weight frequency distributions for each coastal area were obtained by summing, within each size category, the landings from each subarea and depth zone. Plotted serially and fitted with smooth curves, the size-distribution modes traced each brood from its recruitment to its disappearance from the fishery (fig. 11). The curve for each brood is the typical sigmoid curve describing population growth in weight. Its disposition with respect to the ordinate is irrelevant, the midpoints of each size class being arranged arbitrarily theron. In the present report, the procedure of plotting size-distribution modes is carried out only for those population segments occupying offshore areas, portions found on inshore grounds being almost always composed of a single, newly produced brood.

Of the biases associated with the commercial catch-by-size data used herein, that due to different grading practices is potentially the most serious. Two such methods are commonly em-

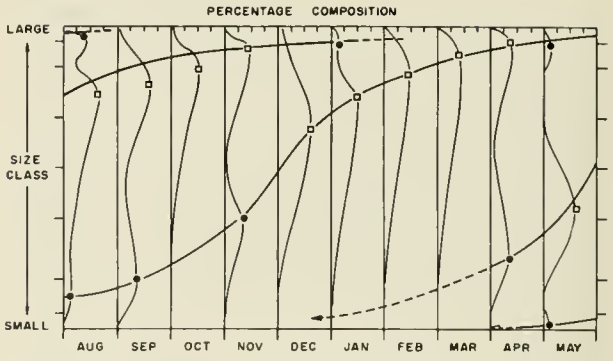

FIGURE 11.—Hypothetical example showing method of delineating shrimp "broods" from weight composition of monthly commercial catches. (Light lines displaced vertically are monthly weight-frequency curves. Squares denote dominant weight-frequency modes. Shaded circles indicate lesser modes. Dark lines displaced horizontally trace progress of individual broods in fishery.)

ployed around the Gulf, viz., "box-grading" and "machine-grading." The former entails taking a representative 5-pound sample of the landing, separating its contents into standard size categories, calculating the proportion in each category, and prorating the landing accordingly. In the latter method, the entire landing is run through a mechanical sorting device.

Grading machines are found at relatively few Gulf ports. But even if available, they may not be used, each fisherman reserving the option of selling his catch on a box-grade basis if he so desires. The problem here is that data of box-graded and machine-graded landings are not comparable for areas in which both methods are used. From the standpoint of getting a true picture of catch size composition, machine-grading is obviously far superior to box-grading. Where machine-graded landings would be expected to yield monthly weight frequency curves truly representative of those of the fishable biomass, or at least of the landings themselves, weight frequencies based on box-graded landings would not, the probability of their exhibiting all modes being quite low. Consolidating the two types of data confounds the net bias and necessitates interpreting weight frequency curves resulting therefrom with some reservation.

INTEGRATION OF DATA

Classical approaches to predicting the yields of, and assessing the effects of artificial and environ-

mental factors on, exploited fish and shellfish stocks incorporate devices known as mathematical population models. In recent years there has developed a specialized branch of fishery biology devoted solely to the measurement of their parameters. These include, in the deterministic sense, the basic constants of fecundity or recruitment, growth, and mortality. Their estimation presents no simple task, and it is significant to note that valid measures of each are contingent upon how well population age structure can be delineated (Watt, 1959, p. 391).

Means for separating commercial shrimp landings into component age classes to secure a picture of population age structure have not yet been devised. Shrimp population research along classical lines is consequently precluded. Differential effects of fishing on shrimp broods at successive ages, relationships between population size and fishing intensity, parent-progeny relationships, and estimation of natural mortality, for example, remain undocumented in statistical terms.

To extract the maximum amount of information on shrimp population status from the kind of data available, the alternative method of generalizing on inferences drawn from graphic integration and interpretation of yield, biomass, and modal-weight curves is employed. Thus comparative trends in yield and biomass should establish, relatively speaking, whether specified stocks adequately maintained themselves during the period over which statistics were collected. Simultaneous data on biomass (age) composition and relative brood strengths aid in reconciling significant deviations in stock mass and, with constant fishing intensity, corresponding fluctuations in yield. The latter information also provides a broader basis for speculating as to how differential fishing on broods making up a given biomass affects their collective potential from the standpoints of yield and reproductive capacity.

POPULATION TRENDS AND CHARACTERISTICS

BROWN SHRIMP

General Occurrence and Features

The brown shrimp is sought in offshore and adjoining inshore waters of the Gulf of Mexico from northwest Florida westward to Mexico. Its commercial range covers approximately 66,000 square (nautical) miles of the Gulf's continental shelf.

Intensive exploitation of the brown shrimp did not begin until the close of World War II. Declining abundance of the industry's mainstay, the white shrimp, prompted a campaign to develop markets for the ever-present brown shrimp, which heretofore had never enjoyed comparable market status. The first catches of any commercial consequence were reportedly made off Texas in about 1947, off Mississippi and Alabama in 1950, and in the Gulf of Campeche in 1951 (U.S. Fish and Wildlife Service, 1958).

During the period 1956–59 this species ranked number one, annually averaging 56 percent (by weight) of shrimp landed at Gulf ports by United States commercial fishermen. In contrast the second- and third-rank species, pink and white shrimp respectively, contributed only 22 and 20 percent. Understandably, the brown shrimp currently attracts most of the attention being given conservation of the Gulf of Mexico's collective shrimp resources.

Over its range of exploitation, the brown shrimp exhibits a pronounced gradient of abundance. Indices similarly derived for all species and areas, and averaged over all months for the years 1956 through 1959, revealed a steady increase from east to west in the mean harvestable biomass of this species (table 6). Maximum stock density now occurs off Texas and eastern Mexico, this being approached in terms of relative density only by pink shrimp fished off southwest Florida and in the Gulf of Campeche. Peak production from its waters marks the Texas coast as the brown shrimp's focal habitat and, coincidentally, the center of the Gulf's extensive shrimp industry.

TABLE 6.—*Mean annual index of fishable biomass—commercial shrimp populations in offshore Gulf of Mexico waters, 1956–59*

Area	Species		
	Brown	Pink	White
Sanibel-Tortugas		0.97	
Apalachicola	0.15	.29	0.24
Pensacola-Mississippi River	.64	.04	.22
Louisana Coast	.52		.45
Texas Coast	.88		.15
East Mexican Coast	1.11		
Obregon-Campeche		.81	
Yucatan Coast [1]			

[1] Not available.

Biologically speaking, the brown shrimp seems to differ little from other commercial species. Taxonomic differences, for example, are quite subtle; and except for minor differences in chronology, events in its morphological development parallel those characterizing life histories of other shallow-water Penaeidae. Ecological factors would therefore be expected to play the dominant if not the more apparent role in separating this species from its relatives. For instance, although the greater proportion of each commercial variety's developing young may temporarily utilize (at different times) the same estuarine habitat, the parents show marked differences in their bathymetric distribution. Thus brown shrimp adults commonly are found on the outer reaches of the continental shelf, suggesting a greater transport distance for newly hatched larvae, and indicating a correspondingly longer migration for juveniles from estuary to offshore spawning ground. In addition, cursory observations tend to support the consensus that a substrate appreciably softer than those ordinarily occupied by its commercial relatives typifies the brown shrimp's habitat (Hildebrand, 1955; Williams, 1958). If the substrate is a major limiting factor, such a requirement may well explain the dominance of this species on the continental shelf from Mississippi Sound westward.

In examining the recent status of the brown shrimp in Gulf of Mexico waters, I view its biomass as a continuous "stock" or population over the range of primary exploitation. However, the possibility of this stock being composed of units or subpopulations enjoying varying degrees of "discreteness" should not be discounted. Though our knowledge in this area is nil, the likelihood of any unit being isolated physically or genetically would seem quite remote. Recent mark-recapture studies in Texas and Louisiana waters indicated, for example, an east to west movement of at least portions of successive generations, each member of which can trace its lineage to a spawning aggregation maintained to the east, presumably in the western part of the Delta area (U.S. Fish and Wildlife Service, 1960; Louisiana Wild Life and Fisheries Commission, 1960).

For convenience in presenting and interpreting data, the brown shrimp stock is divided into two units between which interchange is believed minimized by a natural barrier, namely, the Mississippi River Delta and impinging edge of the continental shelf. Subdivision of the areas lying east and west of the Delta is strictly arbitrary. And although the term "populations" is used freely to identify biomass units within these coastal areas (and subareas), it is used in an artificial sense and in no way implies that actual subpopulations (or "races"), if these exist, have been defined.

Eastern Gulf Populations

Data of fishing effort and yield as related to commercial utilization of brown shrimp populations along the northeastern Gulf coast are given, respectively, in appendix tables 1 and 2. These have been condensed because of space considerations from more extensive tables giving catch-by-depth data on a subarea basis, the subareas involved here being those numbered from 8 through 12 (fig. 1). The two general areas upon which consolidation was based are identified as the Apalachicola and Pensacola-Mississippi River areas. Note that indices used to assess populations or portions of a stock occupying any coastal area were computed from uncondensed data, i.e., data tabulated on a statistical subarea-depth zone basis. Inshore catches are given by specific water body in appendix table 5.

Commercial yield.—During the period 1956–59, brown shrimp production off northwestern Florida (Apalachicola area) was greatly overshadowed by that off Alabama, Mississippi, and eastern Louisiana combined (Pensacola to Mississippi River area) (fig. 12A). Population yields as reflected by commercial landings showed a steady increase from 0.1 to 0.7 million pounds annually in the Apalachicola area, and marked fluctuation between 5.3 and 12.6 million pounds annually in the Pensacola-Mississippi River area. Production in both areas experienced typical midwinter lows and midsummer highs. Although of a much lower order of magnitude, production peaks in the former area occurred slightly in advance of those in the latter.

Fishable biomass.—Comparison of biomass indices revealed upward trends in annual overall brown shrimp abundance from the Mississippi River eastward (fig. 12B). Marked deviations from what might be considered normal fluctuations in seasonal abundance were not apparent. As suggested by the corresponding yield data, a greater biomass, on the average, occupied the more westerly portion of the northeastern Gulf

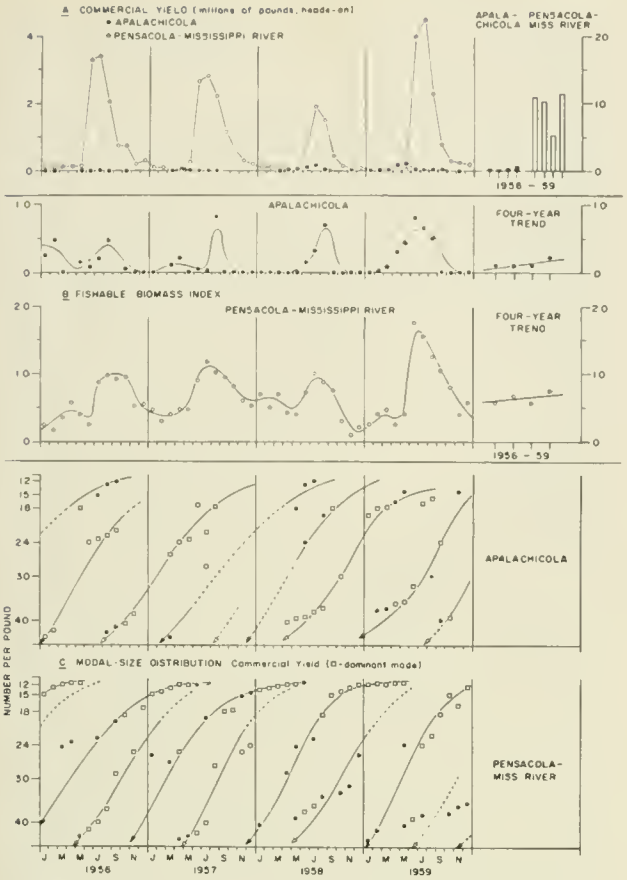

FIGURE 12.—Yield and structure of brown shrimp populations off the northeastern Gulf coast, 1956–59.

coast area. Population cycles as exhibited by biomass curves derived for the Apalachicola and Pensacola-Mississippi River areas showed appreciable similarity except that brown shrimp abundance dropped to a much lower level during the winter months off Apalachicola. This was likely due to the fact that specimens maturing and remaining in this area had already passed out of the range of fishing operations at winter's onset. Whereas the range of year-round exploitation may extend to 45 fathoms in the Pensacola-Mississippi area, it rarely goes beyond 20 fathoms in the Apalachicola area.

Population characteristics.—The brown shrimp population inhabiting eastern Gulf waters evidently produces two broods per year (fig. 12C). Roughly describing population age structure, distribution of modal-sizes comprising monthly yields suggested alternate roles for alternate broods—one "reproductive", one "commercial."

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Those broods forthcoming in late summer and fall (indicated by shaded arrows) are usually of comparatively small size due, perhaps, to reduced survival, increase in weight slowly, and apparently contribute little to the annual yield (cf. figs. 12A, 12B, and 12C). Their residuals, however, seemingly constitute the greater proportion of spawning populations which produce the "commercial" broods in succeeding years. These broods, in contrast, are generated in late winter and early spring (indicated by light arrows), are larger due to better survival during larval and postlarval stages, increase in weight more quickly, contribute disproportionately more to the annual yield (cf. figs. 12A, 12B, and 12C), and, accordingly, make up a smaller proportion of the spawning population. Significantly, late winter-spring broods are harvested at an early age (fig. 12C) with few individuals surviving to maturity. Those that do mature supplement, by virtue of what might be termed "compensatory" growth, the spawning population represented primarily by members of the preceding or fall-winter brood. This relationship is shown in figure 12C where coalescence of members of adjacent pairs of life history curves is vaguely suggested. For the most part, fall-winter broods impart little evidence of existence or strength on the biomass curves until the following fall and winter when their mature elements contribute to small catches. (Note slight modes on curves in fig. 12B during early 1956, 1958, and 1959 in the Pensacola-Mississippi River area.)

Comparative interpretation of figure 12C is rendered somewhat difficult by the paucity of data for the Apalachicola area. Despite this shortcoming, the interrelationships of successive broods still seem sufficiently clear. Causes of variation about the fitted lines do pose a question, however. Part of this variation could be attributed to differential fishing with respect to biomass distribution ("sampling error") and, perhaps, to disproportionate vulnerability or availability of sexes, but most is probably due to the fact that spawning continues in varying degree throughout the year.[3] Even though two peaks of spawning may nearly always be defined, this definition is

[3] One year's (1961) biological sampling on the continental shelf by personnel at the Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas, has revealed the presence in every month of the year of brown shrimp ready to spawn.

often weak due to the magnitude and success of interim spawning being sustained at comparatively high levels. The exact position of one peak relative to the other is therefore difficult to resolve.

The evidence for two broods per year substantiates earlier opinion as to the seasonal reproductive activity in brown shrimp off the upper Gulf coast (Gunter, 1950). Additional evidence in a later section will permit further discussion of this feature of brown shrimp life history.

Inshore population phases.—Up to this point discussion has been limited to the dynamics of offshore phases in the eastern Gulf's brown shrimp population. If attention is turned to inshore phases, parallels to events in offshore population phases may be readily noted.

In both the Apalachicola and Pensacola-Mississippi River areas (but more noticeably in the latter), distributions of monthly commercial yields from offshore and inshore waters correspond very precisely during the period 1956–59 (cf. figs. 12A and 13A). Annual yields fluctuated in like manner although the offshore catches were about twice those of inshore catches.

Closer comparison of curves describing seasonal patterns for offshore and inshore yields from the Pensacola-Mississippi River area reveals that, on the average, peaks in offshore yields lagged slightly behind those in inshore yields (figs. 12A and 13A). This lag reflects the expected pattern for juveniles (spring brood) migrating from inshore "nursery grounds" to parental habitat offshore, pointing up the relationship between inshore and adjacent offshore fisheries and stimulating speculation as to the effect harvesting a brood's prerecruits (in terms of the offshore fishery) could have on attaining the maximum yield from that brood.

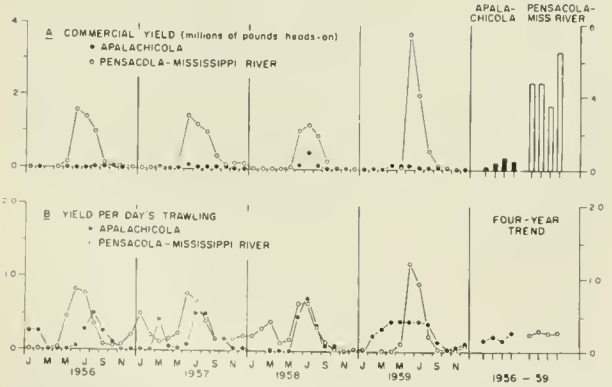

FIGURE 13.—Total and average yield of brown shrimp populations in inshore waters along the northeastern Gulf coast, 1956–59.

Taking into account the species concurrent migratory and growth patterns, it is presumed that such attainment would be realized shortly following egress from inshore waters, or at a point in space and time where shrimp size is equivalent to that at which individuals average about 30 (heads-on) to the pound. The reasoning here derives from an examination of curves in sections B and C of figure 12. Those for the Pensacola-Mississippi River area provide the best points of departure. In 1956 and 1957, maximum population biomass, mainly due to the contributions of late winter-spring broods (light arrows, fig. 12C), was attained during August–September (fig. 12B). Observe now that the brood curves, reflecting average growth of shrimp comprising each brood, exhibit inflections which occurred during the same period. Thus, with growth rates having reached a maximum and the broods themselves attaining maximum weight, biomass from this point on was largely governed by mortality factors. The average size of shrimp at the time of greatest brood mass is shown to have been, as stated above, roughly that at which 30 whole (50 headless) uniform-size individuals weigh 1 pound. In the present example, the greater proportion of shrimp taken by the offshore fleet was, on the average, composed of individuals not much larger than those taken by the inshore fleet.

Corroborating the case for two population broods annually, curves fitted to average monthly yields from inshore waters likewise indicated the occurrence of two broods, one in late summer or fall, the other in late winter or early spring, respectively, the "reproductive" and "commercial" broods referred to earlier (fig. 13B). Moreover, sustained trawling provided crude year-round indices of brown shrimp abundance in the eastern Gulf's inshore waters. These indices suggested, despite lessened reliability of midwinter values, a continuous influx of larvae and tended to confirm the hypothesis of protracted spawning activity. Four-year trends in average commercial yields from inshore population phases closely approximated those derived for offshore phases.

Summary of 4-year status.—During 1956–59, eastern segments of the northern Gulf of Mexico's

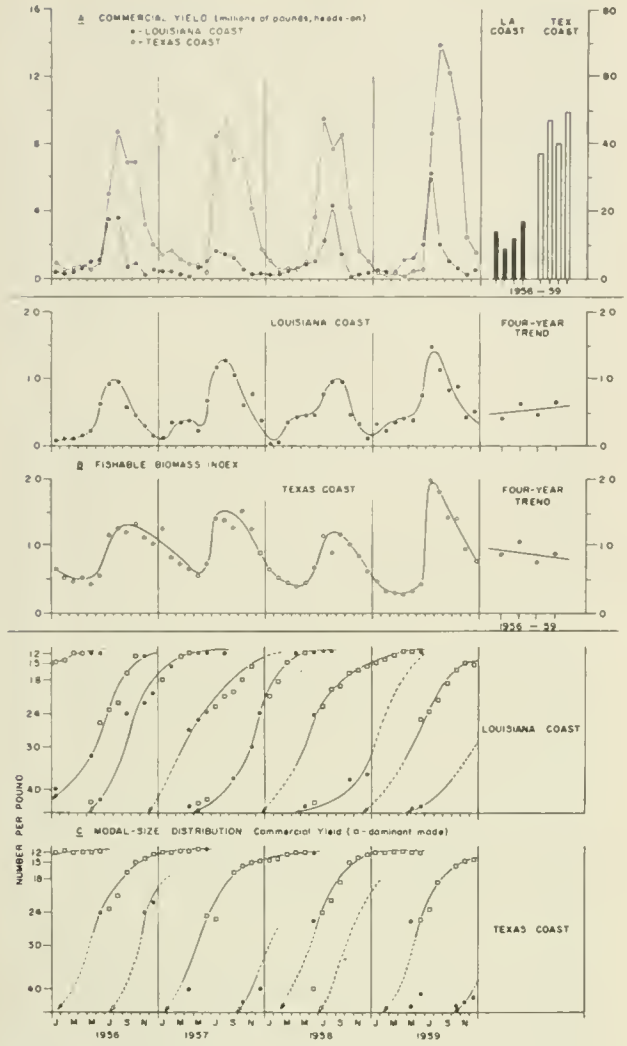

FIGURE 14.—Yield and structure of brown shrimp populations off the northwestern Gulf coast, 1956–59.

brown shrimp stock exhibited no marked departure from the norm obtained for that period. Although commercial offshore and inshore yields diminished significantly in 1958, the corresponding fishable biomass remained at approximately the same level as that attained the 2 previous years. Slightly upward population trends were noted for the 4-year period. Yield composition displayed the same year-to-year pattern. Heavy midyear catches were comprised predominantly of small shrimp, and light late- and early-year catches of comparatively larger shrimp. Assuming intensity of fishing remains more or less constant, i.e., fall-winter broods are not exploited more heavily than past observations indicate,

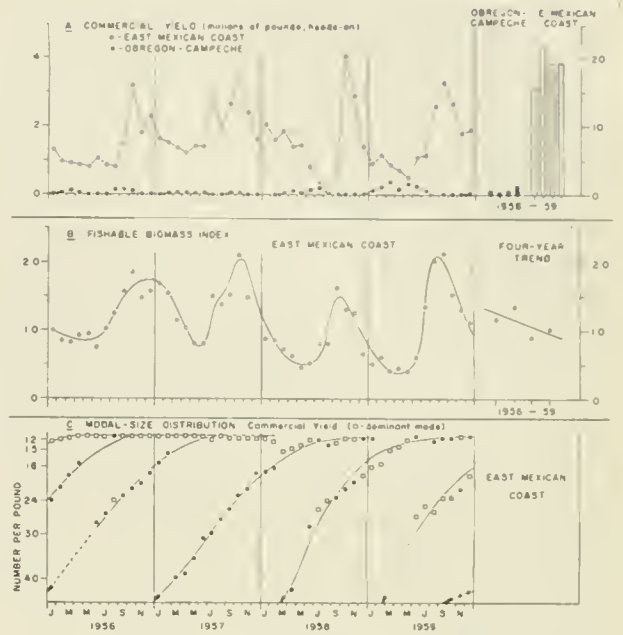

FIGURE 15.—Yield (to United States fishermen only) and structure of brown shrimp populations off the Mexican Gulf coast, 1956–59.

midyear yields of small to medium-size shrimp should stabilize at the 1956–59 level.

Western Gulf Populations

Analysis of western segments of the northern Gulf coast's brown shrimp stock proceeded on a coastal-area basis as before. Commercial effort and catch data for the Louisiana Coast (statistical subareas 13 to 17), Texas Coast (subareas 18 to 21), and East Mexican Coast (subareas 22 to 30) areas are given in condensed form in appendix tables 1 and 2. The latter table also includes small quantities of brown shrimp taken in the Obregon-Campeche area (subareas 31 to 34). Annual landings from specified inshore waters will be found in appendix table 5.

Commercial yield.—Brown shrimp production off the northwestern Gulf coast during the years 1956–59 fluctuated about annual averages of 12.4, 43.3, and 19.3 million pounds, respectively, in the Louisiana, Texas, and east Mexican coastal areas. Landings by the United States fleet ranged from a low of 8.2 million pounds taken off Louisiana in 1957, to a high of 49.4 million pounds harvested off Texas in 1959. Yield trends were up in all areas with Texas exhibiting the steepest climb.

Yield curves again displayed the typical midyear highs and winter lows (figs. 14A and 15A). Com-

parison of curves also revealed the same westward lag in maximum seasonal production noted earlier in the eastern Gulf. Peaks usually occurred during July–August off Louisiana, August–October off Texas, and September–November off eastern Mexico.

Fishable biomass.—Biomass curves derived for western portions of the northern Gulf's brown shrimp stock paralleled those describing eastern portions. Dominant modes of the curve determined from data of commercial operations off Louisiana occurred slightly ahead of or at the same time as those of the Texas curve (fig. 14A). Modes of the curve for eastern Mexico were generally displaced still later (fig. 15A). As also indicated by corresponding yield curves, this suggests a pattern of gross westerly drift for major portions of vernal broods, probably associated with their seaward migration from upper Gulf nursery grounds.

A gradual westward increase in brown shrimp abundance is demonstrated by biomass curves for successive coastal areas being displaced on their ordinates at increasingly higher levels. Four-year abundance trends, on the other hand, exhibited a decline from east to west. Louisiana's available biomass was slightly upward, that off Texas experienced a mild decline, while that off eastern Mexico fell off moderately (cf. figs. 14B and 15B). A pattern thus emerged for the northern Gulf's brown shrimp stock—an upward 4-year trend for eastern segments, a nearly static situation for those centrally located, and a perceptibly downward trend for westernmost segments.

Whether this pattern developed purely by chance or resulted from factors operating differentially yet systematically on adjacent biomass units is problematical. The cumulative effect of a compounded fishing mortality associated with the seasonal westward movement of newly recruited broods is a distinct possibility. Of significance here is the fact that suitable inshore nursery grounds diminish rapidly in extent as one proceeds westward from the Delta. Heavy fishing on broods produced to the east coupled with light recruitment from areas to the west could conceivably result in a systematic population decline from east to west.

It should be noted that biomass curves depicting western portions of the brown shrimp stock may not always be comparable to those describing eastern portions. Commercial fishing off Texas and Mexico, for example, is typically more selective than that off the remaining upper coast. Texas markets are such that small shrimp are ordinarily unacceptable and fishermen consequently avoid landing them, often through discarding, but usually by seeking out aggregations of larger specimens. Moreover, legislation enacted in 1959 encourages fishermen in the Texas Coast area to defer from trawling on predominantly small brown shrimp during June and July by closing coastal waters up to a distance of 10 miles offshore.

Obviously, these factors act to minimize the amount of information yielded by biomass indices computed from commercial statistics. Furthermore, attempts to explain differences in interarea population trends are defeated if fishing practices in adjacent areas are such that resulting statistics lead to incomparable fishable biomass indices. It is quite apparent (fig. 14C) that the definition of fishable biomass as given earlier in terms of "standard" Gulf trawling gear does not hold for all areas.

Population characteristics.—Despite the commercial fishery's tendency toward increased selectivity of larger shrimp on the Gulf's western grounds, catches during 1956–59 periodically consisted of brown shrimp covering a size range sufficient to describe (although somewhat sketchily) the structure of the biomass whose components would ordinarily be vulnerable to the gear employed under conditions of nonselective fishing (figs. 14C and 15C). More specifically, catch composition data included in statistics of fishing activities off Louisiana appeared relatively free of the selectivity bias, whereas those included in statistics of operations off Texas and Mexico did not. The effects of "biased sampling" frequently complicated the picture of population size structure in the latter areas.

Distribution of modes of weight-frequency curves derived for monthly landings taken off Louisiana and Texas provided additional evidence for semiannual brown shrimp broods in upper Gulf waters (fig. 14C). In the western Gulf, however, the timing of each brood's appearance seemed advanced somewhat beyond that of its counterpart in the eastern Gulf, indicating correspondingly later spawning peaks in western areas. This was especially apparent in Texas waters where broods

corresponding to those forthcoming in late summer and fall in eastern waters are generated slightly later, usually during fall and winter.

The coalescence of fall and spring broods described for eastern portions of the upper Gulf's brown shrimp stock was simulated in stock segments lying off Louisiana. However, the relative importance of each brood to the offshore fishery displayed a reversal. Whereas spring broods (light arrows) sustained the commercial fishery to the east, fall or winter broods (shaded arrows) sustained it in the western Gulf, the Louisiana coastal area seemingly being the transition point.

Spring broods in Louisiana waters usually did not contribute measurably to the offshore fishable biomass until late the same year or early the year following. Offshore yields at such times were small but, on the average, composed of mature individuals surviving from the previous spring. Their presence was reflected on the biomass curve by minor, early-year modes (cf. figs. 14A, 14B, and 14C). Dominant modes, on the other hand, invariably indicated the presence, during midsummer, of the stronger fall or winter broods. These contributed the greater portions of annual yields though mean shrimp size during peak harvest (July–August) was somewhat less than that characteristic of spring broods fished during the winter months immediately following their appearance.

Late fall or winter broods also dominated the year-round fishery off Texas and eastern Mexico. Not as well defined in offshore waters as their winter counterparts, spring broods in this area played obscure roles. Their contributions to the offshore fishery were negligible during brood years but probably significant in succeeding years (figs. 14C and 15C). The extent to which spring broods supplement each year's spawning populations remains problematical but there is no question that they sustain important inshore bait fisheries. Lack of appropriate data precludes further discussion.

Factors operating to produce two "generations" of brown shrimp annually are as intangible as their mechanics are complex. But worthy of consideration as an indicator of what underlies this phenomenon is an easily measured environmental parameter, namely, temperature. If the species spawns within an optimum temperature range lying somewhere between annual minimum and maximum temperatures on the floor of the continental shelf, two spawnings per year would be expected; one at some point on the ascending limb of the annual temperature curve, the other at a corresponding point on the descending limb. Taking into account the species capacity for rapid growth, it is reasonable to conjecture further that at least portions of a brood forthcoming at one intercept of the spawning isotherm and seasonal temperature curve would complement the spawning population giving rise to the brood appearing at the subsequent intercept. Until a brood becomes extinct, its residuals would be expected to attain maturity and breed at successive intercepts.

Alignment of periods of maximum spawning intensity with annual sea temperature curves suggests, however, that spawning is associated with seasonal temperature reversals rather than with some optimum temperature. Periods of peak spawning were determined: (1) by extrapolation from brood curves projected backward in time, inferring some knowledge of early growth in penaeid populations (Hudinaga, 1942; Pearson, 1939); and (2) through cursory but systematic observations of ovarian development in spawning populations off the upper Texas coast, such observations being made in the course of research conducted by the Bureau of Commercial Fisheries Biological Laboratory, Galveston Tex. Roughly speaking, heightened spawning activity in the northwestern Gulf's brown shrimp stock seems to occur, on the average, during the period March–April, and again during the period September–October.

Continuous sea temperature data for the northern Gulf shelf are scanty with most of those available representing surface measurements taken at selected shore stations. Lindner and Anderson (1956, p. 621) present comparative bottom temperature curves (inshore; offshore at 3 fm.; and offshore at 10 fm.) constructed from measurements taken during 1931–34 in the Barataria Bay, Louisiana, area. Annual sea temperature curves derived from measurements obtained over extended periods at various other locations are given in figure 16. The more extensive of these, however, reflect conditions in areas some distance removed from what are believed to be principal brown shrimp spawning areas. How well they match seasonal temperature patterns at

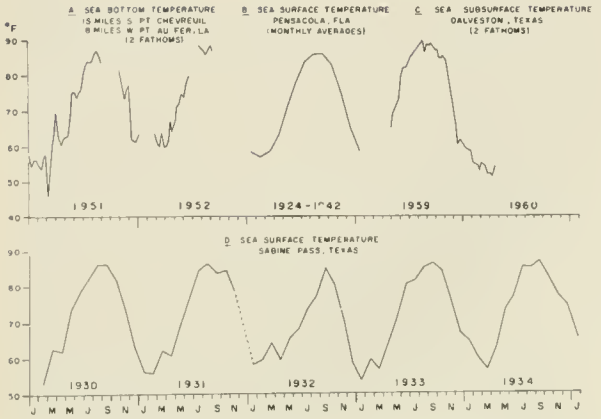

FIGURE 16.—Sea temperatures at selected locations along the northern Gulf of Mexico coast.

Sources: A. and M. College of Texas (1952); A. and M. College of Texas (1955), data collected by U.S. Coast and Geodetic Survey; U.S. Fish and Wildlife Service (Unpublished data); A. and M. College of Texas (1955), data collected by U.S. Fish and Wildlife Service.

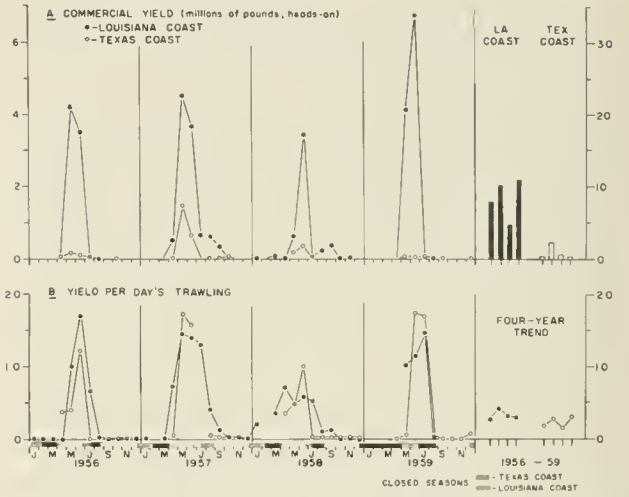

FIGURE 17.—Total and average yield of brown shrimp populations in inshore waters along the northwestern Gulf coast, 1956–59.

20–40 fathoms, is therefore a matter for conjecture.

Assuming reasonable correspondence in the shape and displacement of annual shore-surface and offshore-bottom temperature curves, it may be concluded with the aid of figure 16 that peak spawning activity in the upper Gulf's brown shrimp stock is associated with initiation of: (1) a rapidly increasing rate of temperature change in the spring, and (2) a rapidly decreasing rate of change in the fall.

A knowledge of underlying mechanisms notwithstanding, the fact that semiannual broods sustain the upper Gulf's commercial fishery further complicates brown shrimp population studies. Since successive broods are not subjected to the same environmental stresses, parameters of reproductivity, growth, and mortality may be expected to vary widely from brood to brood and from area to area. This would offer potential difficulty in attempts to project yields on a calendar year basis.

Inshore population phases.—Closed seasons and minimum size limits restrict the annual harvest of brown shrimp from inshore waters of the northwestern Gulf. Most stringently regulated are Texas estuaries from which only negligible amounts (commercial: human consumption) were taken during the 4-year period under study (fig. 17A). Louisiana's inshore catches, on the other hand, were considerably greater but also fluctuated markedly. Actually, average annual brown shrimp production from Louisiana bays approached that of the adjacent offshore fishery and exceeded that of all other inshore waters on the upper Gulf coast. As also noted in the eastern Gulf, annual production maxima for the western Gulf's inshore waters usually occurred slightly before those for offshore waters (cf. figs. 13A and 17A). Comparison of inshore average yield and offshore biomass curves revealed a similar correspondence.

The dynamics of population phases supporting inshore commercial fisheries provoke some interesting speculation about the western Gulf of Mexico brown shrimp stock as a whole. There is no debating the fact that spring broods, first appearing en masse as 3- to 4-week-old larvae at the entrances to inshore waters during late March to mid-April, sustain inshore fisheries for the ensuing 2 or 3 months. Juvenile brown shrimp, for instance, comprised 87 to 99 percent, respectively, of commercial bait shrimp landings from Galveston Bay in June and July, 1960.[4] These shrimp grow rapidly during the inshore phase and, by the time they begin migrating to offshore waters, usually in June and July, they may attain a size equivalent to that at which 42 specimens

[4] Galveston Bay bait shrimp landings for June and July, 1960, totaled 0.20 and 0.15 million pounds, respectively.

(heads on) weigh 1 pound. Their fate after leaving the bays has already been discussed.

But what of the fall broods? Except for representation by small numbers of postlarvae and subsequently an occasional juvenile, they do not appear at entrances to or in inshore waters at the times they might be expected. Commercial trawling, even though greatly reduced at this time, is still sufficient to confirm their presence or absence in inshore waters during late fall and winter months. Where, then, do members of fall or early winter broods pass their prerecruitment phase? The answer, logically, must be: in offshore areas where spawning takes place and mass shoreward transport of eggs and larvae is held to a minimum, or in nearshore areas when unsuitable conditions preclude further movement of developing postlarvae into bays. From the standpoints of brown shrimp population dynamics and management, implications of this apparent phenomenon warrant further attention.

Summary of 4-year status.—For the most part, western portions of the northern Gulf of Mexico brown shrimp stock showed no significant change and all now appear to be in good condition. Over the period 1956–59, the trend in annual commercial biomass was slightly upward in Louisiana waters, absent or only slightly downward in Texas waters, and perceptibly downward in east Mexican waters.

Though typically fluctuating, brown shrimp yields from all waters, except Texas inshore waters tended to rise during the period of study. Notable departures from what might be considered normal fluctuations were the relatively sharp declines in annual yields from Louisiana's offshore waters in 1957 and its inshore waters in 1958. The former can be partly explained by the occurrence and aftereffects of a damaging hurricane which impeded fishing operations during June and July. The latter was due to the relatively poor success of the spring brood of 1958. This, in turn, could also be attributed to hurricane damage in the form of reduced spawning potential and nursery ground capacity.

The downward 4-year trend in fishable brown shrimp biomass off eastern Mexico seemed to be largely due to a low population level in 1958. Figure 15C reveals that large individuals, members of the 2 previous years' fall-winter broods, normally dominated annual yields. Exploitation of broods produced in 1956 and 1957 was restricted to their medium-size and larger components, except in 1957 when shrimp of rather small size helped to make that year's catch the largest of the 4-year period. Assuming constant natural mortality for all fall-winter broods, this had the effect of preventing the 1956–57 winter brood from attaining its potential maximum, thereby resulting in a diminished available biomass during mid-1958.

POPULATION TRENDS AND CHARACTERISTICS

PINK SHRIMP

General Occurrence and Features

During the period 1956 through 1959, catches of pink shrimp averaged 22 percent of all shrimp taken annually from the Gulf of Mexico by United States fishermen. Commercial landings ranged from a high of 48.0 million pounds in 1956 to a low of 30.6 million pounds in 1959 (table 4). Yielding only about one-fifth of the Gulf's overall shrimp harvest, stocks of this species nevertheless constitute the sole support of important fisheries in certain Gulf coast areas.

Although pink shrimp are sought over approximately 56,000 square (nautical) miles of the continental shelf, only one-fourth of this area contributes the preponderance of annual catches. Harvestable concentrations are occasionally found in the northern Gulf, but primary stocks tend to be restricted to its southeasterly perimeter. Specifically, the latter occur off southwest Florida (Sanibel-Tortugas) and northwest Yucatan (Obregon-Campeche), their average densities comparing favorably with or exceeding those calculated for stocks of related species exploited elsewhere in the Gulf (table 6).

Biologically, the pink shrimp differs little from other commercial Penaeidae. Anatomical features are very similar to those of brown and white shrimp. Its life history, except for possible differences in reproductive potential and in timing of events, is also practically identical to theirs, with population development involving an oceanic egg and larval phase, an estuarine postlarval and juvenile phase, and an oceanic adult (progenitor) phase. Growth is also comparable where the pink shrimp occurs with either or both the brown and white species. And, as will be shown in a later section, its population structure is similar.

Ecological features distinguishing the pink shrimp from its close relatives are not well defined.

Cursory observations suggest, however, that whereas adult population segments distribute themselves over the same depth range as that occupied by brown shrimp, maximum density occurs at a somewhat lesser depth. This is particularly apparent in instances where both species inhabit the same general area. But, as speculated upon earlier when discussing the distribution of brown shrimp, the underlying factor may be substrate composition. On the basis of extensive field observations, Hildebrand (1955) concluded that over the same bathymetric range, brown shrimp prefer a very soft mud substrate and pink shrimp a somewhat harder and coarser bottom. A similar conclusion was reached by Williams (1958), who conducted substrate selectivity experiments under laboratory conditions with juveniles of both species. As additional factors controlling the distribution of littoral Penaeidae, food preferences or habits as they relate to substrate type should not be discounted.

Pink shrimp, like brown and white shrimp, also display a marked tendency to move to deeper water with advancing age (Iversen, Jones, and Idyll, 1960). This movement presumably occurs, for the most part, over substrate characterizing the species habitat.

The Sanibel-Tortugas Population

Undergoing intensive exploitation for the first time about 1950, the pink shrimp population occurring off southwest Florida has since supported a valuable commercial fishery. Arbitrarily delimited, its habitat extends coastwise from the vicinity of Tarpon Springs on the north to just beyond the Keys on the south (fig. 6). The seaward limit at all points has been set at the 45-fathom contour although population fragments may be found in deeper water. Within these boundaries the population disperses itself over a projected bottom area of some 23,000 square nautical miles with Florida Bay and adjacent estuaries serving as "nursery" grounds for its immature phases. Studies are currently being undertaken to determine whether the population is actually continuous as presumed, or whether it is separated into two discrete units at about the 26th parallel.

Commercial fishing on the Sanibel-Tortugas grounds now continues with varying intensity the year round (fig. 18). Spatial distribution of

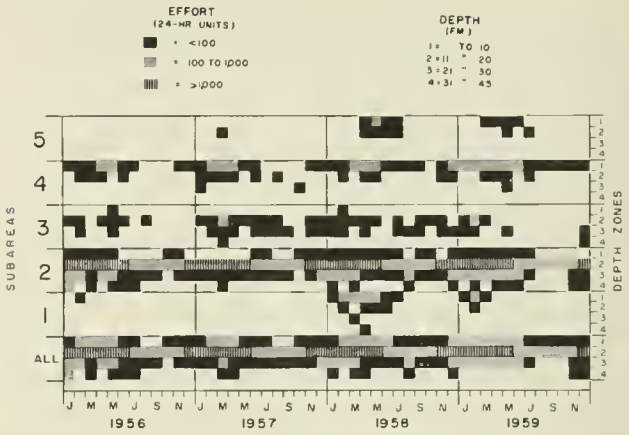

FIGURE 18.—Distribution (schematic) of fishing effort in the Sanibel–Tortugas area, 1956–59.

trawling effort follows a somewhat regular pattern. Greatest concentrations occur between 5 and 25 fathoms just north of the Dry Tortugas (statistical subarea 2) and in 5–15 fathoms off Sanibel Island (subarea 4). Operations are gradually extending to intermediate and outlying areas though untrawlable bottom precludes intensive fishing in many of these.

Condensed data of commercial effort and landings for the Sanibel-Tortugas area are given in appendix tables 1 and 3, respectively.

Commercial yield.—Over the period 1956–59, annual pink shrimp production in the Sanibel-Tortugas area fluctuated about an average of 19.2 million pounds, this representing about 11 percent of the total Gulf production of all species. Landings ranged from a high of 24.7 million pounds in 1958 to a low of 13.9 million pounds in 1959. Despite a practically constant expenditure of effort, the 4-year production trend was down appreciably, its slope reflecting an average decline of about 1.5 million pounds per year. Particularly interesting is the fact that the catch of 1958 was the largest ever recorded for the so-called Tortugas fishery, and that of 1959 the second lowest (cf. Idyll, 1957, table 4). This dramatic drop together with a long-term waning trend in production have stimulated concern for the fishery's future welfare.

The yield curve derived from monthly landings reveals that peak production in the Sanibel-Tortugas fishery is attained during winter and early spring (November–May), 80–85 percent of each calendar year's catch being made in that period

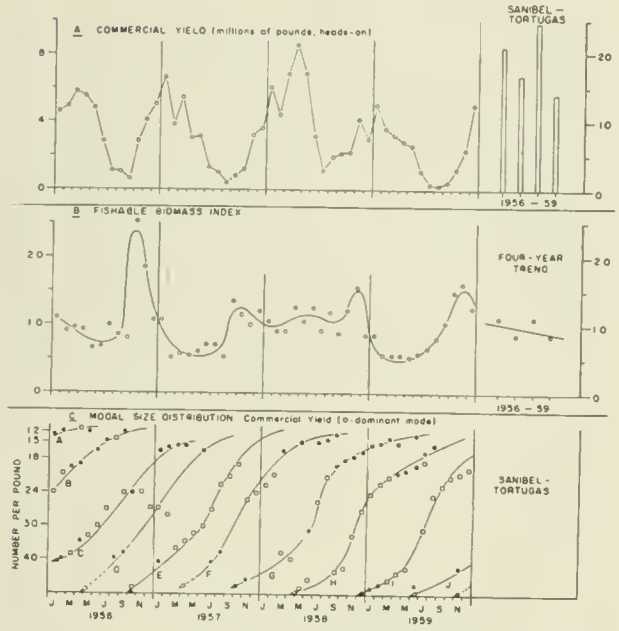

FIGURE 19.—Yield and structure of the pink shrimp population off the southwest Florida coast (Sanibel–Tortugas area), 1956–59.

(fig. 19 A). This seasonal pattern contrasts with those of upper Gulf coast fisheries wherein production normally reaches a maximum during late summer and fall months.

Fishable biomass.—A plot of monthly catch-per-unit-intensity values suggests that the Tortugas population's fishable biomass maintained itself within fairly narrow limits during the better part of the 4-year study period (fig. 19B). As would have been expected, seasonal deviations did occur, their analysis providing, perhaps, the principal clues in defining causes for the fishery's attrition. Meriting special attention are the reduced population levels sustained through the early months of 1957 and 1959, together with a perceptibly downward population trend during the 4-year period.

A comparison of figures 19A and 19B indicates little correspondence between yield and fishable biomass other than a suggestion that low annual yields seemed to occur in years when the population maintained itself at minimum levels. Yields considerably lower than average paralleled low biomass levels during the early portions of 1957 and 1959, the relationship in the latter year constituting the most noteworthy example. Although the population during 1956 and 1958 remained at levels appreciably higher than those in 1957 and 1959, it is not unreasonable to conjecture that excessive fishing in each preceding year could have contributed to the low population levels and hence yields in the years respectively succeeding them.

Population characteristics.—Semiannual periods of peak spawning activity, already indicated for stocks of other Gulf species, seem to be typical of Sanibel-Tortugas pink shrimp as well. These are revealed by serial plots of (catch) size composition data which are believed reasonably descriptive of the population's actual size or age structure (fig. 19C). Production of broods indicative of peak spawning activity corresponded rather well with that noted for brown shrimp off the northeastern Gulf coast, spawning evidently taking place in late winter or early spring (light arrows) and in late summer or early fall (shaded arrows).

On the other hand, intrayear variation in relative brood strengths appeared negligible, contrasting sharply with the great seasonal variation typical of brown shrimp broods produced along much of the upper Gulf coast. The degree of exposure to exploitation at different stages of brood development did vary seasonally, however. This is indicated in figure 20 where crude estimates of the absolute contributions of each brood at successive developmental stages are graphically shown. These estimates were obtained by merely subdi-

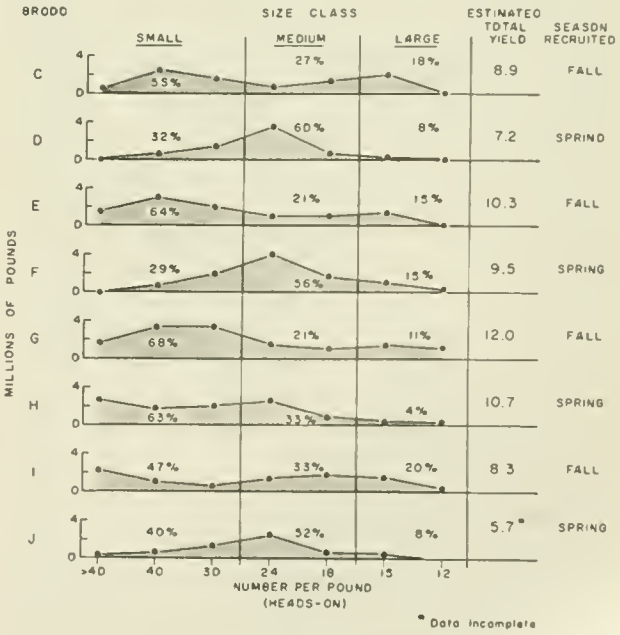

FIGURE 20.—Relative yields per brood by size class—Sanibel–Tortugas pink shrimp population, 1956–59

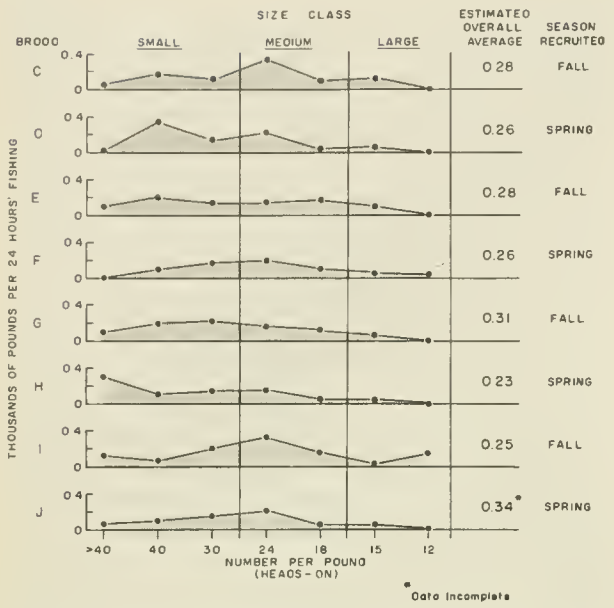

FIGURE 21.—Yield per 24 hours' fishing by brood and size class—Sanibel–Tortugas pink shrimp population, 1956–59.

viding monthly landings at the low, intermodal points on corresponding weight frequency curves. Note that those broods recruited in the fall ordinarily yielded the greater portion of their virtual biomass at juvenile (small) stages, whereas those recruited in the spring yielded most heavily at more advanced stages. A similar but not as pronounced pattern is reflected in figure 21 which depicts the average weight by size class contributed by each brood at successive life history stages. The relative uniformity of average "small-shrimp" catches yielded by broods considered in this study suggests a correlation between availability of newly recruited broods (small shrimp) and the amount of effort expended in their capture. Since peak fishing traditionally occurs shortly after its appearance, the fall brood is subjected to comparatively disproportionate exposure at such times. Evidence suggests that the degree of exploitation suffered by broods at and for a short period following recruitment not only governs the magnitude of fluctuation in annual yields but controls their composition as well.

Growth in fished (or recruited) portions of the Sanibel-Tortugas population was fairly uniform during the 4-year study period. Assuming delineation of successive generations in figure 19C is reasonable, members of broods recruited in the spring, on the average, grew slightly faster and attained maturity earlier than members of broods recruited in the fall. The former required an average of 13 months contrasted to the latter's 15 months to grow from a size equivalent to 31–40, to 9–12 shrimp to the pound. A growth differential between sexes is recognized for commercial Penaeidae (e.g., Lindner and Anderson, 1956), but its manifestations in the present analysis are obscured. Sex composition data would have permitted an evaluation of the effects of a variable sex ratio on growth patterns in the total population.

Summary of 4-year status.—The Sanibel-Tortugas pink shrimp stock evidenced more sensitivity to the mechanics of exploitation than any stock thus far examined. Causes of widely fluctuating and declining annual yields despite a relatively static effort expenditure can be traced to differential fishing on broods immediately following their recruitment. This is reflected in what appears to have been a progressively greater demand for and utilization of small shrimp during the 4-year study period (fig. 22). The net result has been a corresponding downward trend in stock biomass (fig. 18B), the dependent fishery at the same time being subject to varying availability and inconsistent quality in terms of size of shrimp harvested. In striving to obtain higher and higher production, operations and general economy have had to depend more and more on harvests of small, non-premium shrimp. Unfortunately, information on the value of landings taken annually from the Sanibel-Tortugas stock is not available for trend study. But Idyll (1957) stated that the fishery's annual net profits reportedly showed a gradual decline for the years 1953 through 1956, even though production in the latter year represented an alltime high. Indications are that the trend has not changed.

Examples of how recent patterns of exploitation have contributed to the present status of the Sanibel-Tortugas fishery may be readily provided. As previously stated, relatively heavy fishing on small post recruits visibly curtailed the expected potential of certain broods. For instance, note in figure 19C that brood "H" was fished comparatively hard immediately following recruitment (cf. fig. 19A), and at a period when the total pink shrimp biomass was at a reduced level (fig. 19B). To reiterate, peak biomass ordinarily occurs

during early and midwinter (fig. 19B) with the major portion of each calendar year's catch being made during and for a short time following this period (fig. 19A). But although brood "H" sustained early 1959 production, it did so at an appreciably reduced level, the consequence being that the catch in 1959 was the lowest in recent years. Moreover, its quality was lessened because the fishery had to rely upon very small shrimp belonging to the subsequent brood, "I".

This gross analysis is clarified somewhat in figures 20 and 21, which roughly delineate absolute and average yields by size classes for successive broods. In both figures, the serial relationships

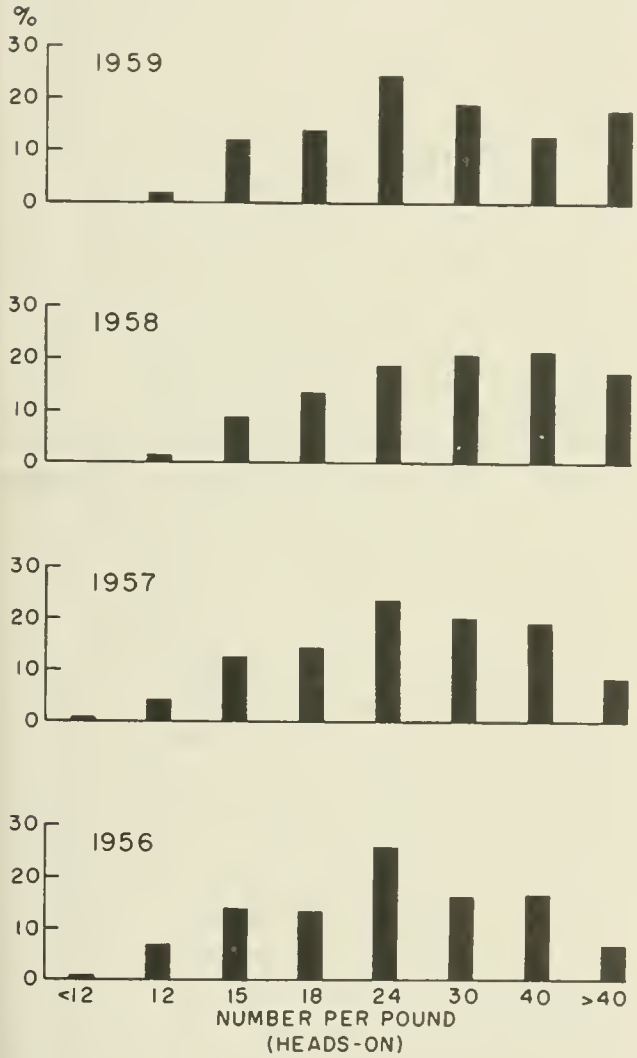

FIGURE 22.—Relative size composition of commercial pink shrimp landings from the Sanibel-Tortugas area, 1956–59.

inferred above are reasonably clear. Harvest of small shrimp [35 count (whole) and smaller] in excess of that amount presumably compensating for natural mortality markedly reduces the expected yield of premium shrimp. Unfortunately, measurement of each brood's biomass at recruitment was impossible, thereby precluding provision of a basis for comparing broods and for studying the effects that varying fishing intensities at different developmental stages had on total brood yields. With controlled fishing, however, a yield curve such as described by brood "F" (figs. 20 and 21) would appear to approach that which is most desirable from the standpoint of achieving maximum utilization of the resource. Note that its mode occurs at the 25–30 (41–50 heads-off) count-size range, the point on the population growth curve where the rate seemingly reaches a maximum.

The foregoing explanation of the Tortugas fishery's 4-year decline was founded on the premise that within- and between-year recruitment remained fairly constant. This assumption is not refuted upon gross examination of available data. The problem then was one of deciding at what stage of population growth the resource should be cropped so as to obtain the maximum virtual yield. No mention was made of the possibility that the Tortugas stock on the whole was being overfished although a continuation of present trends might justify its speculation. Up to the present stage of development in the Tortugas fishery, the pink shrimp population supporting it has displayed great resiliency in overcoming any adversities that might have been associated with exploitation. Presumably, the species high reproductive potential and the relatively undisturbed state of its inshore nursery grounds have thus far offset any incursions due to fishing on the mature stock. On the one hand, this suggests the likelihood that environment control could enhance the carrying capacity of estuarine waters in which immature shrimp undergo early development, with annual recruitment and yields being supplemented accordingly. On the other, it stresses the importance of protecting existing nursery areas from ill-advised modifications, and carefully regulating the take of juvenile shrimp there. However, the possibility of excessive fishing on the mature stock resulting in levels of reproduction below those

approaching nursery ground capacity should not be discounted.

Upper Gulf Populations

Pink shrimp play a comparatively minor role in the penaeid species complex characteristic of the northern Gulf coast. Only along the more easterly reaches do they enter commercial catches in any quantity, and then with very irregular frequency. In some areas, especially in Texas, pink shrimp are bought and sold as brown shrimp. Such a practice masks the actual contribution of this species to local fisheries, and at certain seasons may seriously bias data of brown shrimp landings as well.

Condensed statistics of trawling effort and pink shrimp landings in the Apalachicola and Pensacola-Mississippi River areas are given in appendix tables 1, 3, and 5. Trace amounts of pink shrimp taken in areas west of the Mississippi River are also recorded in table 4.

Commercial yield.—Yields of pink shrimp from offshore waters in the Apalachicola and Pensacola-Mississippi River areas averaged about 7 percent of all shrimp taken annually in these areas during the period 1956–59. Production in the Apalachicola area fluctuated widely between a maximum of 2.1 million pounds in 1958 and a minimum the following year of only 11,000 pounds (fig. 23). Landings originating in waters off Alabama, Mississippi, and eastern Louisiana collectively showed a steady decline from a 1956 high of about 0.8 million pounds. Production in both areas closely followed the seasonal patterns typical of related species, reaching a maximum during the spring or early summer. The largest quantity of pink shrimp taken elsewhere off the upper Gulf coast was 0.1 million pounds caught off Texas in 1958. As noted earlier, this figure (as well as landings of the same species in other years) is too low due to misclassification of the pink shrimp in the Texas coast area.

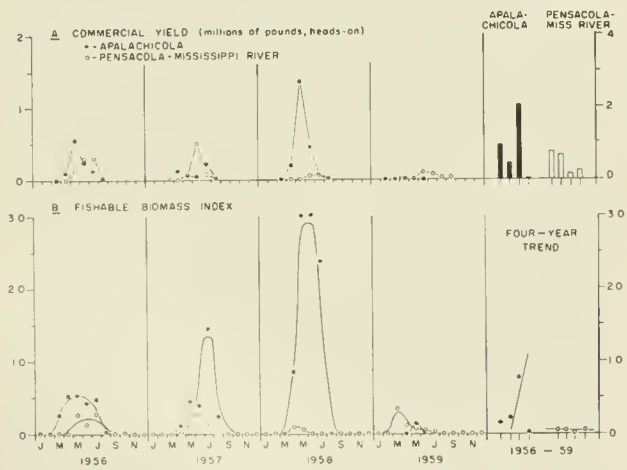

FIGURE 23.—Yield and biomass of pink shrimp populations off the northeastern Gulf coast, 1956–59.

Fishable biomass.—Limited data provide a sketchy picture of offshore populations during the 4-year study period. For the pink shrimp population off Apalachicola, they indicate a significant buildup in strength during 1956–58, followed by a dramatic and inexplicable decline in 1959 (fig. 23B). Peak abundance of small to medium shrimp occurred annually during May–July with especially large quantities available in 1957 and 1958. There is general similarity in pink shrimp yield and population patterns between the Sanibel-Tortugas and Apalachicola areas (cf. figs. 19 and 23), stimulating conjecture as to population continuity in the eastern Gulf.

As expected on the basis of low yield, biomass indices reflected a correspondingly low level of abundance for pink shrimp occupying the waters between Pensacola and the mouth of the Mississippi River (fig. 23B). Seasonal modes occurred either slightly in advance of, or at about the same time as those observed for the Apalachicola area. Year-to-year variation in their magnitude was insignificant, there being no evidence of a population trend during the 4 years of study.

Inshore population phases.—Even less noteworthy than its offshore status was the pink shrimp's status in adjacent inshore waters. Bays and estuaries in the Apalachicola area yielded a maximum of only 416,000 pounds in 1957, and those in the Pensacola-Mississippi River area a maximum of 196,000 pounds in the same year (fig. 24A). Annual landings held fairly steady in both areas with the exception of a sharp 1959 dropoff in the Apalachicola area. Pink shrimp in catches from inshore waters were outweighed by brown and white shrimp in almost every instance. Inshore waters contributing to the northern Gulf's commercial shrimp fisheries are shown in appendix table 5.

The seasonal occurrence and relative density of pink shrimp in inshore waters of the Apalachicola and Pensacola-Mississippi River areas may

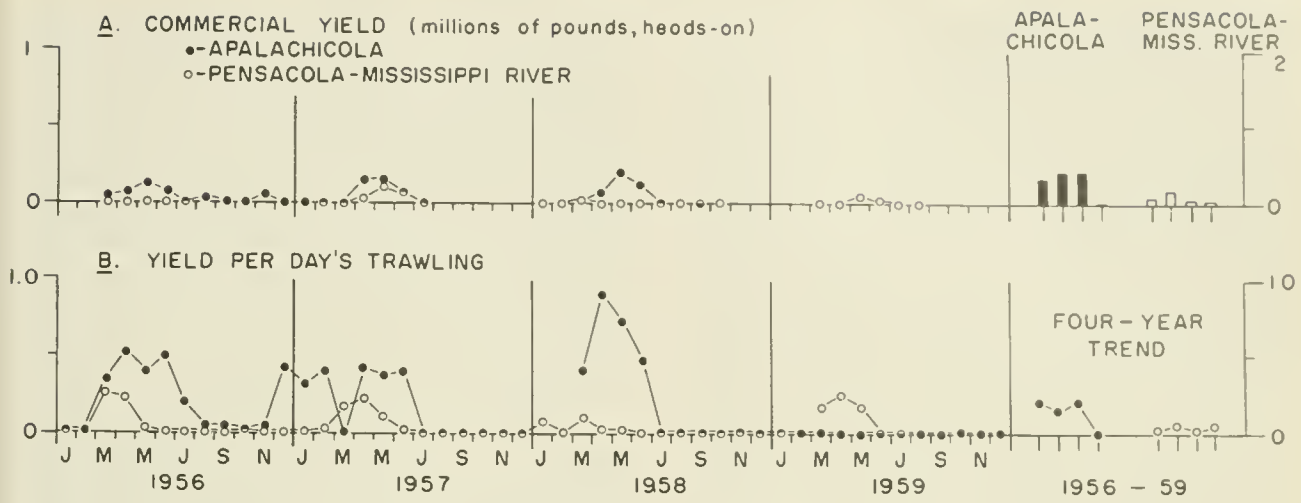

FIGURE 24.—Total and average yield of pink shrimp populations in inshore waters along the northeastern Gulf coast, 1956–59.

be inferred from serial plots of average catches (fig. 24B). Larvae evidently begin appearing on the inshore nursery grounds toward the end of the calendar year. Growth to a fishable size is attained late the same winter and early the following spring. That migration from inshore waters is well underway by May is corroborated by concurrent increases in offshore catches. By the end of August pink shrimp have practically disappeared from inshore waters. Data on size composition of catches made in adjacent offshore waters are inadequate to prove whether or not more than one period of peak spawning activity occurred each year, but they suggest a single peak extending over a period of 1 or 2 months.

Summary of 4-year status.—Except for 1958, pink shrimp contributed little to upper Gulf coast fisheries. Four-year population trends were either very pronounced and meaningless due to widely fluctuating population levels (Apalachicola), or nonexistent with populations holding steady at very low levels (Pensacola-Mississippi River). All data point to the fact that the pink shrimp's commercial range extends no farther westward than the Apalachicola area.

The Gulf of Campeche Population

Shrimp stocks lying off the northern coast of Yucatan, although reconnoitered by the Japanese as early as 1936, were not fished significantly until the close of World War II. Operations on the so-called Obregon-Campeche grounds by United States vessels began about 1950 and have steadily expanded ever since.

Three species of Penaeidae support the Gulf of Campeche fishery. Brown and white shrimp are found in commercial quantities off Tupilco and Obregon (statistical subareas 31 and 32), while pink shrimp predominate north of Carmen and west of Campeche (statistical subareas 33–35). No United States fleet activity in the Yucatan Coast area (statistical subareas 36–40) has been reported in recent years.

On the basis of comparisons with data supplied by the Mexican Bureau of Fisheries and Allied Industries for the years 1956 and 1957, the Mexican fleet accounts for about 56 percent of all shrimp harvested annually in the Campeche area (appendix table 6). Reflecting to some extent a respect for Mexico's claim to a 9-mile territorial limit, the United States fleet takes only about 6 percent and 1 percent, respectively, of the total brown and white shrimp harvest, but almost 65 percent of the total pink shrimp catch. United States vessels concentrate their activities on the extensive flats within a radius of 15 to 80 miles west of Morros Point.

Statistical coverage of the fleet fishing the Obregon-Campeche grounds is complicated somewhat by the fact that trawlers completing a trip may land portions of catches of as many as a half dozen other trawlers still on the fishing grounds, and only a fraction of what they themselves caught while away from port. This very

efficient system of "freighting" (or transshipping), wherein vessels stagger their departures to and from the distant Campeche grounds, greatly enhances the quality of shrimp arriving at United States ports, but renders difficult the problem of assigning effort and catches to individual trawlers. Fortunately, most of the Campeche fleet operates out of a few Florida and Texas ports where statistical agents, with the full cooperation of the fishing industry, have devised effort and catch accounting methods so effective that statistics of United States fleet operations in the Gulf of Campeche may be included among the most accurate of all statistics describing the Gulf shrimp fishery. Such statistics, condensed from more extensive tables, are given in appendix tables 1 and 3.

Commercial yield.—After reaching a high of about 33 million pounds in 1953, annual landings of Campeche pink shrimp by United States fishermen stabilized at 24–25 million pounds over the period 1954–56 (Idyll, 1957, table 4). Thereafter (1957–59), they steadily declined to a low of 13.4 million pounds in 1958 but then began to climb again, reaching 16.4 million pounds in 1959 and about 18 million pounds in 1960. The lowest annual take recorded prior to 1958 was 8–9 million pounds in 1951, early in the fishery's development.

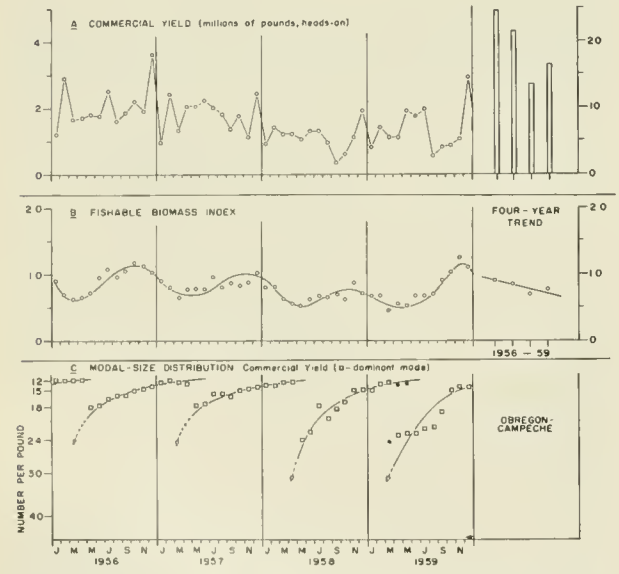

FIGURE 25.—Yield (to United States fishermen only) and structure of the pink shrimp population off the Mexican Gulf coast, Obregon-Campeche area, 1956–59.

In contrast to seasonal catch patterns in most shrimp producing areas, the 1956–59 pattern for pink shrimp on the Campeche flats showed relatively steady year-round production (fig. 25A). Greatest month-to-month variation occurred during midwinter with the highest monthly production in December and (until fall catches dropped below "normal" in 1958 and 1959) the lowest in January. This sharp drop is believed to reflect intensification of adverse fishing conditions rather than marked seasonal changes in shrimp abundance.

Fishable biomass.—Here, as in the case of the Texas brown shrimp fishery, the definition given "fishable biomass" does not hold. This is due to the rather rigid restrictions concerning the sizes of shrimp landed that the fishery imposes upon itself. The United States fleet fishing the Campeche pink shrimp population is, perhaps, the most selective of any comparable unit operating in Gulf waters. Rarely are Campeche landings composed of a predominance of shrimp smaller than 19–24 heads-on count size. And only in recent years has the average size landed fallen below 16–18 whole shrimp to the pound. The task of maintaining quality control, i.e., sorting the decreasing numbers of large shrimp from increasing catches of small shrimp, is reportedly becoming more and more difficult. The consequence of such practices is that landings are not representative of that portion of the population ordinarily vulnerable to the gear employed, and interpretations given analyses of associated statistics apply only to members occupying the upper size or age strata.

Involving only the population phases comprising shrimp equivalent to 19–24 count size (heads-on) and larger, a plot of monthly biomass indices for the period 1956–59 yields the seasonal abundance curve typical of Gulf shrimp populations (fig. 25B). Its amplitude of relatively low order can be attributed to the fact that landing statistics pertained solely to older population segments, the curve itself in no way reflecting actual status of the greater part of pink shrimp aggregations occupying the grounds. Thus the most useful conclusions that can be drawn from figure 25B are that available quantities of premium pink shrimp on the Campeche flats reach a seasonal peak during the fall, and,

during the 4-year study period, experienced a significant decline.

Population characteristics.—Little information on population age structure could be obtained by plotting weight composition modes of monthly Campeche landings. As intimated above, weight composition curves were almost exclusively unimodal with large shrimp predominating at all times (fig. 25C). Conclusive evidence of more than one period of heightened spawning per year is lacking, but bimodal weight-frequency curves for spring landings in 1959 suggest that two peaks in annual spawning activity may also be characteristic of the Campeche pink shrimp population.

Summary of 4-year status.—Accurate but restrictive statistics gave only a vague picture of conditions in the Campeche pink shrimp population. Composed primarily of large-size shrimp, yields to United States fishermen declined sharply over the period 1956–58, but increased measurably during the next 2 years. Of significance was the drop in apparent abundance of large shrimp commencing in 1958 and sustained through 1959. Whether this was caused by excessive fishing alone, or by a combination of fishing and adverse environmental conditions, will always remain problematical. The Campeche fishery serves as a good example of one in which a lack of all-inclusive yield data (i.e., landings plus discards) inhibits proper population analysis. If landing statistics truly represented what was actually caught, further investigation of the Campeche population's dynamics would be justified.

POPULATION TRENDS AND CHARACTERISTICS

WHITE SHRIMP

General Occurrence and Features

Once the primary objective of commercial shrimping interests, the white shrimp now occupies a relatively minor position in the Gulf of Mexico's overall shrimp picture. For many years it constituted the sole support of a thriving fishery in bays and bayous along the Louisiana-Texas coast. There was no need to venture into the open Gulf until about the mid-1930's when prospects of an expanding market prompted the fishery's extension. The offshore fishery then developed rapidly, reaching its zenith in the mid-1940's. Gradually, however, and for reasons not yet clear, domestic white shrimp supplies diminished to the point where related species began to attain competitive status. Accelerating production of brown and pink shrimp from newly discovered domestic and foreign grounds finally overtook that of white shrimp in the mid-1950's. The former two species have since maintained a superior position.

During the period 1956–59, white shrimp ranked third behind brown and pink shrimp, annually averaging but 20 percent of all shrimp taken from Gulf waters by United States fishermen. Although subordinate on a Gulfwide basis, this species, like the pink shrimp, still sustains local fisheries in certain coastal areas.

Because of its longer history as a commercial species, the white shrimp has been studied more extensively than all other species combined. Nevertheless, there is still much to be learned about its life history and habits. Taxonomically, the white shrimp is very similar to the brown and pink shrimp although distinction between it and either of the latter two species is more clear-cut than that between the brown and pink shrimp themselves. Aside from their timing, events in the white shrimp's life history follow the same sequence and otherwise simulate those characteristic of littoral penaeids. Growth appears comparable to that of closely related varieties where they and the white shrimp are subject to similar ecological stresses. Reproductive potential is also believed to be approximately equivalent though much uncertainty prevails concerning shrimp fecundity. Actual egg counts have never been made for any species, but ova production in the white shrimp has been estimated without any indication of statistical reliability. King (1948) mentions "* * * the half million or so eggs which the average female will produce * * *"; Anderson, King, and Lindner (1949) state that "A count made by the authors on the ripe ovaries of a female, 172 mm. total length with spermatophore attached, revealed a total of approximately 860,000 eggs"; Lindner and Anderson (1954) specify that "A female will lay about 500,000 eggs at each spawning . * * *"

As already noted, when two or more species occur in the same general area, littoral Penaeidae may also be discriminated on the basis of apparent ecological requirements. Substrate quality has

been cited as a major factor in brown and pink shrimp distribution; white shrimp likewise are thought to distribute themselves accordingly (Hildebrand, 1954; Williams, 1958). Notwithstanding the fact that generations produced by each species may undergo early development on the same inshore nursery grounds, the displacement of adult population segments in offshore waters is reasonably discrete. Whereas pink shrimp adults tend to occupy sand-shell bottoms of firm consistency, brown and white shrimp are most often found on much softer bottoms, typically soft clay, mud, or terrigenous silt. Substrates inhabited by the latter two species are difficult to differentiate but a second factor, bathymetry, helps to resolve the problem. Contrasted to their deep-water counterparts, mature white shrimp are ordinarily found only in the nearshore shallows (0–15 fm.), sometimes even in those portions of inshore waters nearest the sea. Whether or not substrate and bathymetry are the major factors governing distribution of littoral Penaeidae on the continental shelf remains problematical.

White shrimp occur in widely varying quantity at nearly every point on the Gulf's continental shelf. A notable exception is that portion of the shelf lying off southwest Florida (statistical subareas 1–4). Commercial concentrations are well defined in humid or semi-humid areas bordered by extensive estuarine complexes. One such area is that lying between Tupilco and Carmen on the east Mexican coast. Here a fairly dense population of white shrimp, fished in Gulf of Campeche waters by the Mexican fleet, seems to be associated with numerous coastal lagoons, especially the Laguna de Terminos. The most important commercial concentrations, however, occur in and off the northern Gulf coast marshes between Apalachicola and central Texas, with peak population strength being attained in and adjacent to Louisiana's vast estuarine complex (table 6).

Although most white shrimp are taken from 20 fathoms or less, the species may occasionally be found at depths up to 45 fathoms (Springer and Bullis, 1952). The 45-fathom contour is therefore taken as the approximate seaward limit of the species range. In addition, the northern Gulf of Mexico stock is arbitrarily subdivided into those units lying east and west of the Mississippi River Delta. Commercial statistics of effort and production (1956–59) are given in condensed form by months and depths for all coastal areas in appendix tables 1 and 4. Inshore production by specific water body is summarized for the same period in appendix table 5.

Eastern Gulf Populations

Commercial yield.—Over the period 1956–59, white shrimp annually averaged 13 percent by weight of all shrimp taken commercially from offshore waters in the Apalachicola and Pensacola-Mississippi River areas. Landings ranged from a low of 1.2 million pounds in 1957 to a high of 2.0 million pounds in 1959.

Production in the Apalachicola area was relatively stable, mildly fluctuating between 0.3 and 0.5 million pounds annually. Landings from the Pensacola-Mississippi River area were more erratic, dropping from 1.7 million pounds in 1956 to 0.7 million pounds in 1957, and then climbing again to 1.7 million pounds in 1959 (fig. 26A). Seasonal landing patterns for both areas show that each year's white shrimp production peaked approxi-

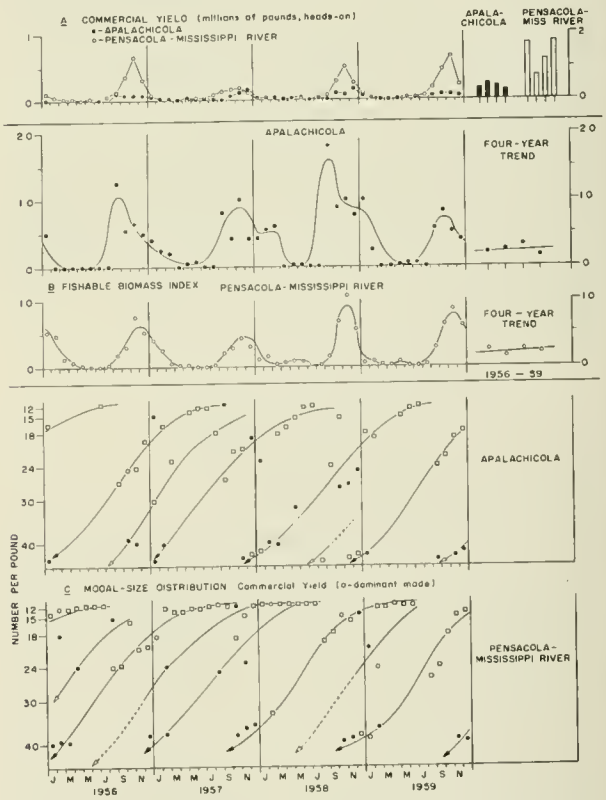

FIGURE 26.—Yield and structure of white shrimp populations off the northeastern Gulf coast, 1956–59.

mately 5 months after brown shrimp production reached its highest level (cf. figs. 12A and 26A). Larger sizes of shrimp (40 or less whole shrimp to the pound) nearly always predominated during periods of maximum offshore production (October–December).

Fishable biomass.—Population density curves exhibited the same pattern of seasonal fluctuation already described for other exploited shrimps (fig. 26B). Greatest white shrimp biomass, with which peak commercial production coincided, occurred in both areas toward the end of each calendar year. Although white shrimp biomass in the Apalachicola area usually exceeded that in the Pensacola-Mississippi River area during corresponding periods of maximum density, greater expenditures of effort for larger and more available shrimp resulted in greater yields from the latter area. Annual levels of fishable biomass were comparable for both areas, as were the 4-year trends which indicated a slight overall population rise.

Population characteristics.—Despite rather sketchy data, semiannual spawning in the northeastern Gulf's white shrimp stock was suggested by modal-size distributions derived from monthly landings (fig. 26C). Spawning is evidently protracted throughout much of the year but, using time of recruitment as a point of reference, heightened activity appears to take place during late spring and early summer (shaded arrows), and again in late fall and early winter (light arrows). This contrasts with a similar phenomenon noted for the coexistent brown shrimp stock in which corresponding periods of peak spawning occur somewhat later, respectively, in late summer and late winter.

Relative strengths of age classes generated through intensified spawning at the beginning and close of the annual reproductive season (late spring-early winter) varied considerably. Broods forthcoming at the season's beginning (shaded arrows) were consistently larger and obviously played the dominant role in sustaining the stock and thus the fisheries dependent upon it. Remnants of broods produced during later stages of the annual spawning season, while apparently contributing little to either offshore or inshore fisheries, probably aided in population maintenance by complementing spawning populations. The comparatively greater strength of early-season broods is emphasized on the corresponding 4-year biomass curves (cf. figs. 26B and 26C). Seasonal modes reflected the occurrence of these broods in the form of (1) recruits-of-the-year and (2) 1-year-old adults, the proportion of each group varying from year to year. Modes largely representing late-season broods are barely noticeable.

Early-season reproductive classes themselves experienced appreciable year-to-year variation both as to time of recruitment and size at recruitment. The former is attributable only to varying environmental conditions, whereas the latter could be due to the cumulative effects of fishing and undue environmental changes. Any deleterious effects of fishing, if operative, were so vague as to be undetectable. But the possible effects of large-scale environmental changes warrant some comment.

The question arises, for example, as to whether the intense storm systems which lashed the Gulf coast west of the Delta in June and August, 1957, could have caused substantial environmental changes in areas as far east as the Pensacola-Mississippi River area. Landings of white shrimp from offshore and inshore waters, as well as the species' overall population level, were down markedly in this area during the last half of that year (figs. 26–27, A and B). The decline becomes more dramatic when it is noted that effort expended in offshore and inshore waters during the period July–December was down only 17 and 5 percent, respectively, from that expended during the same period in 1956, while corresponding white shrimp

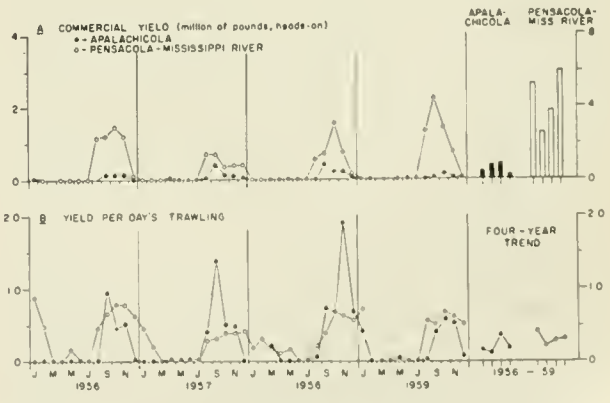

FIGURE 27.—Total and average yield of white shrimp populations in inshore waters along the northeastern Gulf coast, 1956–59.

landings were down 61 and 53 percent. The low 1957 yield must therefore be attributed more to a reduction in population size and availability than to poor fishing conditions and hence widespread reduction of fishing operations during the season of peak white shrimp density. Population reduction, in turn, may well have been attributable to poor survival in the early-season spawning class of 1957, excessive mortality having occurred during larval and inshore phases when adverse environmental conditions (high tides and extensive flooding, excessive turbulence, etc.) due to severe storms could be expected to exact the greatest toll.

On the average, growth rates in white shrimp populations fished off the northeastern Gulf coast were lower than those in populations off the northwestern Gulf coast. A more comprehensive discussion of growth in upper Gulf white shrimp stocks is deferred to a later section.

Inshore population phases.—During the period 1956–59, conditions in the northeastern Gulf's inshore fisheries for white shrimp very nearly paralleled those in adjacent offshore fisheries. Differing chiefly in amplitude, seasonal and annual yields in the Apalachicola and Pensacola-Mississippi River areas experienced the same order of fluctuation (figs. 26A and 27A). Seasonally, peak production of small shrimp in inshore waters occurred 1 to 2 months earlier than that of somewhat larger shrimp in offshore waters.

White shrimp comprised, on the average, about 45 percent by weight of all shrimp taken from inshore waters in both areas. Annual inshore landings in the Apalachicola area averaged 1.5 times corresponding offshore landings, and ranged from a high of 0.9 million pounds in 1958 to a low of 0.3 million pounds the following year. In the Pensacola-Mississippi River area the differential between inshore and offshore landings increased to a factor of 3.2, with inshore landings ranging from a high of 5.8 million pounds in 1959 to a low of 2.5 million pounds in 1957.

Crude indices of seasonal white shrimp density on inshore grounds reemphasize the dominant role played by early-season spawning classes (fig. 27B). Peak biomass is attained during the period September-November and occurs slightly in advance of maximum seasonal biomass in contiguous offshore waters (cf. fig. 26B). This reflects continuous migration of juveniles from inshore to offshore waters during that period. Late-season spawning classes are barely evident in figure 27B as very small modes recurring annually during April-May in both areas and in most years.

Summary of 4-year status.—White shrimp production exhibited similar patterns in offshore and inshore fisheries during the period 1956–59. No 4-year trend was evident in the Apalachicola area, but a very steep upward trend following substantial declines in 1957 was noted for fisheries in the Pensacola-Mississippi River area. Inshore production of small shrimp consistently exceeded offshore production of larger shrimp in both areas.

Four-year trends in overall relative density were comparable for offshore and inshore population phases, being slightly up in both areas. No relationship between intensity of fishing on either inshore or offshore population phases and total yields in the same and subsequent years was apparent. The greatly reduced catch of white shrimp from the Pensacola-Mississippi River area in 1957 is at least partly attributed to the side effects of intense storm systems which hit the coast just west of the Mississippi River Delta in June and August of that year. Extensive flooding due to abnormally high tides and excessive runoff is hypothesized as having caused higher-than-normal inshore mortality in 1957's early-season spawning class.

Fluctuations in white shrimp population strength and yield appeared to be largely governed by environmental factors. Provided these do not attain extreme proportions, and effort remains constant or does not greatly exceed recent expenditures, white shrimp landings in the Apalachicola and Pensacola-Mississippi River areas should stabilize at the same or just below levels recorded for the period 1956–59. There is some indication that white shrimp in the Apalachicola area could, on the average, withstand slightly heavier exploitation.

Northwestern Gulf Populations

Commercial yield.—The northwestern Gulf of Mexico annually surpasses all other areas in the production of white shrimp. Highest yields have been consistently obtained from that portion of the coastal stock inhabiting Louisiana's offshore and inshore waters.

In each of the years 1956 through 1959, the Louisiana Coast area contributed, on the average,

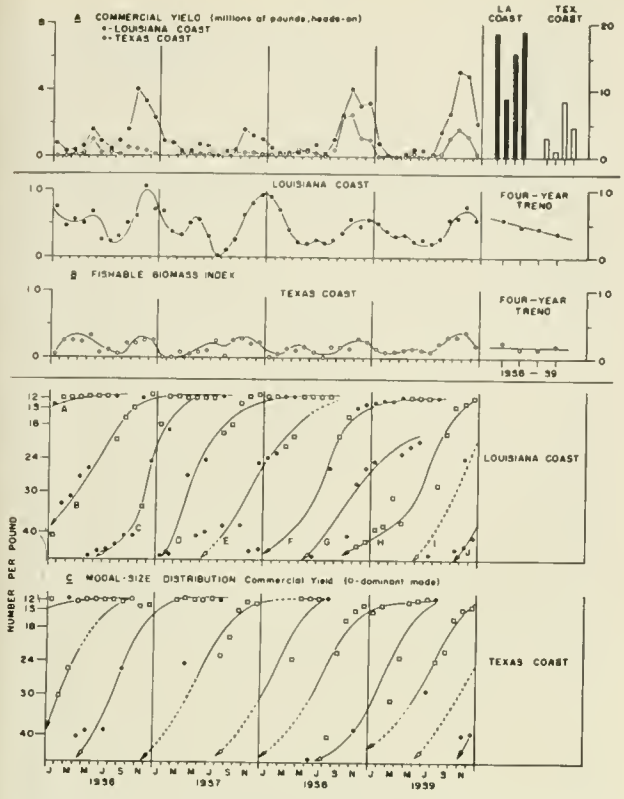

FIGURE 28.—Yield and structure of white shrimp populations off the northwestern Gulf coast, 1956–59.

72 percent of all white shrimp taken off the United States Gulf coast. Of all species harvested offshore within the area itself, white shrimp averaged 51 percent. Landings ranged from a low of 7.7 million pounds in 1957 to a high 17.9 million pounds in 1959 (fig. 28A). The 1957 catch represented a 55-percent drop from the level of the previous year and restimulated widespread concern for the white shrimp's future welfare (Viosca, 1958). Annual landings have since recovered, however, and in 1959 exceeded those of 1956. But, present status of the white shrimp notwithstanding, the question: "What caused the long-term decline from a 1945 production peak of well over 110 million pounds?" [5] remains unanswered.

Ranking second in offshore production, the Texas Coast area contributed 20 percent of the white shrimp taken commercially each year off the United States Gulf coast. This constituted but 9 percent of the weight of all species harvested annually from offshore waters within the area itself. Landings ranged from 1.0 million pounds in 1957 to 7.8 million pounds in 1958 (fig. 28A).

Seasonal distribution of white shrimp landings in the Louisiana and Texas Coast areas differed slightly from that noted in areas east of the Delta. Peak offshore harvest took place annually about a month earlier (in October as contrasted to November), and at the same time as or immediately following peak brown shrimp production. In addition, a secondary production mode usually occurred in May.

Fishable biomass.—Because size selectivity biases appeared minimal and all vulnerable sizes therefore reasonably well represented, biomass indices derived from offshore fishery statistics are believed to give a reliable picture of white shrimp population strength in the Louisiana Coast area. This was not the case in the Texas Coast area where purposive fishing for only the larger shrimp sizes was again evident. Seasonal distributions of biomass indices for both areas compared as to position of modes on the time axes but differed as to amplitude and relative displacement on the quantity axes (fig. 28B). The fishable stock off Louisiana maintained a higher average level over the 4-year period, 1956–59, but fluctuated more widely within and between seasons than did that off Texas. Despite increasing yields, the former apparently suffered a comparatively severe setback in 1957 from which it has not yet recovered. The Texas stock, on the other hand, has remained nearly stable, its fluctuating yields being largely attributable to vicissitudes of the industry, abundance of other varieties, etc. Midyear modes which were barely evident on biomass curves derived for the Apalachicola and Pensacola-Mississippi River areas show quite prominently on the Louisiana and Texas curves.

Since seasonal modes on biomass curves for adjacent statistical areas were usually positioned at corresponding points in time, coastwise drift of white shrimp juveniles migrating seaward is considered to have been negligible.

Population characteristics.—Evidence for two annual periods of increased spawning activity in upper Gulf coast white shrimp stocks is amplified in figure 28C. Good representation of vulnerable

[5] Data taken from "Fishery Statistics of the United States—1956", Statistical Digest No. 43, U.S. Fish and Wildlife Service, 1958. Since large-scale exploitation of the brown shrimp was not yet underway, practically all of this production is assumed to have consisted of white shrimp.

sizes in Louisiana landings provides a synoptic picture of population size structure in what is considered the nucleus of these stocks. Heightened spawning in November–December and in June–July may be inferred, respectively, from offshore recruitment surges in May–June (light arrows) and again in November–December (dark arrows). This pattern is quite similar to that described for populations in the northeastern Gulf. Year-to-year variation in extent of maximum spawning activity and timing of recruitment is again obvious; but a major distinction when comparing reproductive patterns for stocks in both areas is the enhanced significance of late-season broods (light arrows) to offshore and inshore fisheries in the northwestern Gulf areas. Secondary yield and biomass modes occurring in May or June (figs. 28A and 28B) are attributed in large part to late-season broods supplementing remnants of the prior year's early-season brood (fig. 28C). Populations giving rise to early- and late-season broods are believed to be predominated by survivors of the previous year's corresponding broods. The degree of predominance appears to vary widely, however, being largely dependent upon the relative initial strength and subsequent survival of each brood comprising a spawning population.

The foregoing description of the white shrimp's seasonal reproductive pattern agrees to some extent with that already given by Lindner and Anderson (1956). Also in general accord with the findings of these authors are gross conclusions that may be drawn from figure 28C regarding growth in recruited (offshore) population phases. If this figure gives a reasonably faithful picture of spawning class progress, note on curves tracing broods in populations fished off Louisiana that growth in weight is, on the average, comparatively slow during the period November–April. This agrees with statements made by Lindner and Anderson (1956) who used increase in body length rather than increase in weight as the growth criterion. By means of tagging experiments they showed that white shrimp of most sizes (105–175 mm. total length) ordinarily fished by the offshore fleet experienced reduced growth during winter months, and that growth during this season was approximately constant regardless of size. Over the remainder of the year, growth rates, as would be expected, were much greater in the smaller sizes (105–125 mm. total length at release) than in the larger sizes (155–175 mm. total length at release).

Compared to rate of growth measured in terms of length, rate of growth in weight is fairly low in the small sizes, increases to a maximum somewhere in the middle of the shrimp's overall size range, and then tapers off as the maximum attainable size is approached. Using increase in weight as the growth criterion and maintaining correspondence with Lindner and Anderson's results based on length increments, note in figure 28C that seasonal growth varied from year to year. Thus the late-season spawning class of 1955 (Louisiana Coast, brood B) apparently grew more rapidly the following November–April (1956–57) than did those of 1956 and 1957 (broods E and G) during the winters of 1957–58 and 1958–59, respectively. Average size in the 1956 class, for example, only increased from that equivalent to 24, to not quite 16 whole shrimp to the pound over the period December–April, about a 30 percent weight increase. This is contrasted to a 150 percent increase in average weight for the 1955 class during the corresponding season a year earlier.

The principal lesson derived here is that population growth in white shrimp (and very likely other species as well) is dynamic and therefore difficult to predict. Mark-recapture studies can only contribute growth estimates derived over short periods of time from a limited number of individual animals. Such estimates may be questionable not only from the standpoint of overall representativeness, but also from the standpoint of expected consistency in space and time. Before resource productivity can be projected, average growth in populations treated as units and broken down insofar as possible according to their component age classes, is the factor demanding measurement. This is best achieved in the case of exploited populations through analyses of appropriate commercial statistics. Current statistics, unfortunately, provide only a crude or "qualitative" picture of population growth. Progressive elimination of data biases should provide increasingly accurate growth parameter estimates together with some indication of their expected variability. For the present, however, eye estimates of optimum growth from serial alignment of what are considered representative weight-frequency distributions must suffice.

Figure 28C suggests that maximum rate of growth in the northwestern Gulf of Mexico white shrimp stock, although varying in magnitude from generation to generation, occurs, on the average, somewhere within that size range having limits equivalent to the weights at which 25 to 30 individual whole shrimp weigh 1 pound (41–50 count, heads off). This compares with evidence as to size at which growth in weight reaches a maximum in the northeastern stock, as well as in the Gulf's major stocks of brown and pink shrimp. But because information concerning natural mortality rates is lacking, answers to the question: "Where on the population growth curve do weight losses due to natural mortality begin to offset weight gains due to growth?" cannot be given. If natural mortality from the juvenile stage upward proves negligible, harvesting should be restricted to shrimp whose growth rate is approaching or has reached a maximum. Should natural mortality prove appreciable, utilization at a smaller average size may be indicated.

As in the case of northern Gulf of Mexico brown shrimp populations, semiannual periods of intensified spawning activity in coexisting white shrimp populations defy explanation. The mechanics of physiological adaptation to a highly variable environment are not understood, but temperature is believed to be a major if not the primary factor governing spawning activity in littoral Penaeidae. This relationship has already been considered in discussing the reproductive cycle of the brown shrimp. It was concluded that heightened spawning in brown shrimp populations off the northern Gulf coast was related to seasonal temperature reversals and not to some fixed "optimum" temperature.

A similar conclusion may apparently be drawn for the white shrimp except that increased spawning activity seems more closely related to reduction in rate of temperature change as seasonal minimum and maximum temperatures are approached. This can be construed to be in agreement with Lindner and Anderson (1956), who make the very general statement: "Spawning in Louisiana appears to be more closely associated with rising and falling temperatures than with absolute temperature."

Inshore population phases.— Over the period 1956–59, white shrimp comprised about 45

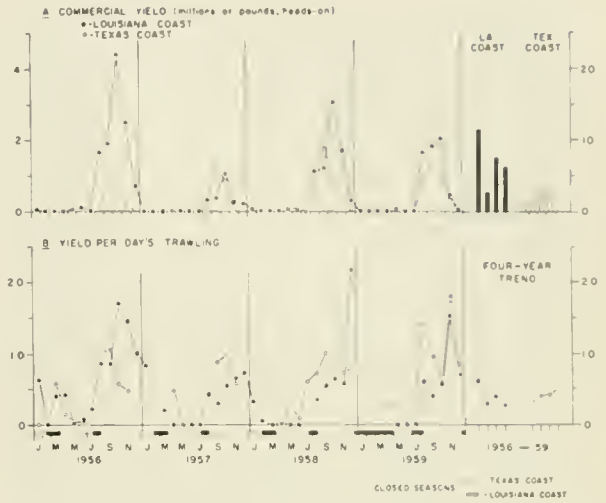

FIGURE 29.—Total and average yield of white shrimp populations in inshore waters along the northwestern Gulf coast, 1956–59.

percent of all shrimp taken annually from inshore waters in the Louisiana and Texas Coast areas. Inshore catches usually accounted for about one-half of all white shrimp taken in the former area, and two-thirds of that harvested each year from the latter area. Yearly white shrimp landings from Louisiana's inshore waters fluctuated between a high of 11.4 million pounds in 1956 and a low of 2.8 million pounds the following year. Inshore landings from the Texas Coast area ranged from a low of 1.3 million pounds in 1956 to highs of about 3.6 million pounds in 1958 and 1959 (fig. 29A). Prospects for the Texas inshore fishery are encouraging. On the basis of incomplete data for 1960, the upward production trend established during 1956–59 is being maintained.

A negative production trend signified by the decrease in Louisiana's 1957 inshore landings was countered with legislative action in the form of closed seasons more stringently enforced than those previously in effect. Accordingly, laws closing inshore waters of the State to all shrimping from the beginning of July to mid-August [6] and again from mid-December to the end of the following April, went into effect in 1958. Production in the offshore white shrimp fishery has since recuperated nicely, but the trend in the inshore fishery is still far from that desired.

[6] The "spring" season was extended to mid-July in 1960.

Enactment of such laws obviously implies that excessive fishing on certain population segments was or could have been primarily responsible for the fishery's downfall. Indeed, Viosca (1959), without any supporting evidence or explanation of probable mechanics, blames overfishing along with the 1952–57 drought. Aided by fairly complete and up-to-date statistics, one can now better speculate as to what did cause the demise of the Louisiana white shrimp fishery in 1957, and whether or not the aforementioned laws have been or will be effective in bringing about its recovery.

Closed seasons during the 4-year study period precluded complete pictures of white shrimp density patterns on inshore trawling grounds in the Louisiana and Texas Coast areas. As already mentioned, Louisiana exercised spring and winter closures beginning in 1958. From 1956 through 1958, Texas restricted large-scale commercial operations on its inshore waters to the periods March–mid-July and September–mid-December. In 1959 it eliminated the "spring" season and restricted commercial bay operations to the period mid-August–mid-December.

Despite resulting discontinuity, abundance curves derived for inshore population phases in both areas nevertheless suggest the occurrence of two annual modes (fig. 29B). A continuous curve for the Louisiana Coast area in 1956 and a practically complete curve for the Texas Coast area in 1958 verify a spring surge in abundance (April–May), and a dominant fall wave with peak varying annually between the months September to December. Close correspondence between catch and abundance patterns for inshore and adjacent offshore fisheries emphasizes, as Lindner and Anderson (1956) also point out, the proximity of inshore and offshore environments constituting white shrimp habitat. In contrast, the time lapse in migration from inshore to offshore grounds is considerably greater for brown shrimp due to the greater distances involved. Seasonal density and yield for the latter species, as shown earlier, reach a maximum in offshore waters a month or more following peak abundance and catch in contiguous inshore waters.

Annual and 4-year trends in white shrimp abundance on the northwestern Gulf's inshore grounds generally corresponded to those describing population phases on offshore grounds (cf. figs. 28–29 A and B). The significant feature in every case but one was the sharp drop in overall population levels in 1957, inshore phases in the Texas Coast area apparently escaping the effects of whatever caused the widespread decline. These effects manifested themselves through markedly reduced white shrimp production in inshore and offshore fisheries as far east as the Pensacola-Mississippi River area.

Failure of the 1957 fisheries in the Pensacola-Mississippi River area has been partially attributed to the poor success of that year's early season spawning class. Side effects of intense storms striking the coast west of the Delta were, in turn, conjectured as having been the cause. Since these storms centered in the Louisiana Coast area, it is hypothesized further that they contributed in even greater degree to population damage and production decline there. Thought to have wrought the most damage was hurricane "Audrey" which hit the coast just east of the Louisiana–Texas border on June 27. Storm surges brought tides of almost 14 feet above mean sea level (m.s.l.) in the Cameron, La., area; 4 feet above m.s.l. in Garden Island Bay, La., 250 miles to the east; and 3 feet above m.s.l. at Port Aransas, Tex., 220 miles to the west. Low-lying areas in Louisiana were inundated up to 25 miles inland (Moore and staff, 1957). Tropical storm "Bertha", not quite attaining hurricane intensity, shortly followed "Audrey", striking the coast in the same general area on August 9. The highest accompanying tide, 4.7 feet above m.s.l., was recorded in Vermilion Bay, La.

The occurrence of these storms coincided with periods of peak inshore and nearshore concentrations of (1) migrating juveniles representing the 1956 late-season brood, and (2) late postlarvae and juveniles representing the 1957 early-season brood. Although the mechanics involved are obscure, it is conceivable that factors such as: extended periods of high salinity, destruction of cover and food supplies, and excessive turbulence, all induced by extraordinarily high tides, acted corporately to disperse and otherwise exert greater-than-normal mortality in white shrimp populations during vulnerable inshore phases.

Excessive fishing on spawning populations giving rise to late-season and early-season broods in 1956 and 1957, respectively, is discounted as a

contributing factor. Comparatively speaking, indices of mean biomass for offshore and inshore population phases suggested that white shrimp spawning potential in 1956 and early 1957 was more than adequate.

Although effort expenditure fell off during the latter half of 1957, the decline was not sufficient to account for the disproportionate drop in landings. Effort expended on inshore and offshore grounds in the Louisiana Coast area during July–December, 1957, was 72 and 51 percent, respectively, of that expended during the same period in 1956. Corresponding landings, on the other hand, were only 25 and 36 percent of those recorded in 1956. About the same amount of effort expended in Texas offshore waters during the latter half of 1956 was recorded for 1957, but the corresponding white shrimp catch declined 43 percent. In contrast, the Texas inshore fishery doubled its production of white shrimp during the same period with only a 55-percent increase in effort expenditure. Most of this, however, came from bays along the southern half of the Texas coast, outside the main area of storm damage.

Significantly, brown shrimp landings from Louisiana's offshore waters were off 43 percent in the last half of 1957 despite expectations of as successful a spring brood for that year as was produced the previous year. Note however, that this drop was not out of line with the 49-percent drop in corresponding effort expenditure. Recall also that overall mean population biomass during 1957 was up in all northwestern Gulf areas. In fact, brown shrimp landings from offshore waters in the Texas Coast area increased 15 percent over those for 1956. All evidence thus suggests that coexistent brown shrimp populations did not suffer the effects of those factors to which the demise of the white shrimp population was attributed. Reduction of brown shrimp catches off Louisiana (July–December, 1957) must therefore be considered a result of a proportionate decrease in shrimping effort brought about by extended periods of unfavorable operating conditions.

A similar conclusion cannot be drawn for the western Gulf of Mexico white shrimp stock and the fishery it sustains. Record low landings from Louisiana waters in 1957 must be ascribed more to a real decline in population strength than to relaxed exploitation during a period when the white shrimp normally attains peak density and availability. The import of factors contributing to this decline is also manifested in the magnitude of the following year's landings. Thus, notwithstanding an immediate return of effort expenditure to its 1956 level (figs. 8 and 10), restoration of landings to their former level has lagged for 2 years.

The effectiveness of newly enacted closed-season laws (inshore waters: Louisiana, 1958) in bringing about this recovery appears questionable. Most noteworthy, perhaps, is the fact that these closures generally coincide with or occur shortly after seasonal ebbs in the white shrimp's nursery ground phases. Records show that in years prior to enactment of the latest and most effective closed-season law (1956–58), white shrimp landings (inshore) over the period January–April, and December, averaged but 6 percent of each year's total. The closed season, mid-December through April, in effect, protects (1) residuals of early-season spawning classes, most of whose representatives will have already passed to offshore waters by the time the fishing season closes, and (2) late-season broods, the postlarvae of which begin to move into inshore areas at about the same time. Most members of the less important late-season classes will have attained commercial size when the fishing season reopens in May. Though now protected on inshore areas, these classes have never contributed significantly to inshore or offshore fisheries.

On the other hand, early-season broods which are fished heavily in inshore waters during late August through November are the same broods dominating the offshore fishery which reaches peak production almost simultaneously. They support the white shrimp fishery but are not now afforded anywhere near the extensive protection given late-season broods.[7] Nor is additional protection called for *unless* a significant relationship between fishing rate and brood size (or recruitment) manifests itself.

Available statistics do not permit establishing whether or not such a relationship prevailed. But, despite improved yields, the white shrimp stock in the northwestern Gulf has shown little sign of recuperating from the 1957 ebb. This

[7] The closed season mid-July to mid-August offers early-season white shrimp broods protection from excessive fishing on precommercial sizes. Inshore production of brown shrimp has not been affected by either closure.

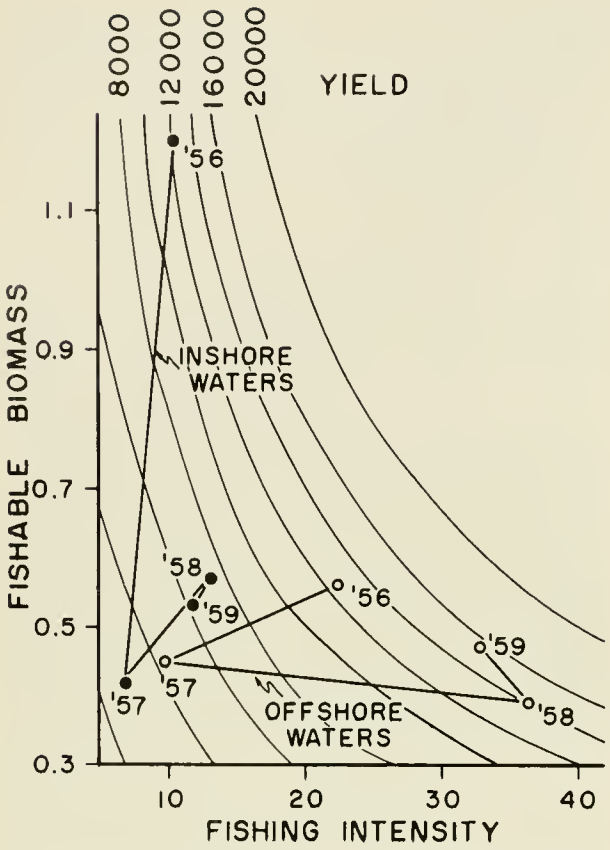

FIGURE 30.—Relationship between fishable white shrimp biomass and fishing intensity in successive early-season spawning classes, Louisiana Coast, 1956–59. [Yield is in thousand-pound units.]

could be due to too heavy fishing pressure having been exerted too soon after extreme population setbacks. If each year's dominant early-season spawning classes are roughly separated by analyzing only those statistics for the months July–December, plots of mean annual biomass against corresponding fishing intensity mildly suggest such a possibility (fig. 30). In Louisiana's offshore waters, quadrupled fishing intensity in 1958 had the apparent effect of delaying initiation of a recovery trend until the following year. Unfortunately for the white shrimp, 1958 was a year in which record high shrimp prices induced extra-heavy fishing to recover losses suffered the preceding year. Most of this was directed at brown shrimp with the low-level white shrimp population suffering coincidentally. Effects of exploitation inshore are also well illustrated and, in fact, may well have been the controlling factors. A doubling of the fishing intensity in 1958 seemingly contributed to the decline in the offshore population phase the same year, and in itself may have stifled an earlier upsurge in the overall population. Relaxation of fishing pressure on the inshore phase in 1959 resulted in concomitant recovery in offshore (spawning) population phases.

In summary, the question is not so much one of whether, following periods of high natural mortality, fishing intensity should be regulated at all, but one of deciding at what season such regulation would be most effective. Little benefit can be expected from suspending fishing in inshore waters when population phases there are at minimal density. On the other hand, closed seasons in offshore waters supporting multispecies fisheries are out of the question altogether.

Summary of 4-year status.—White shrimp production in the Louisiana and Texas Coast areas experienced a sharp drop in 1957. Since then, trends in the more important offshore and inshore fisheries have been up, but return to 1956 production levels has been slow. Incomplete data for 1960 indicate that former high levels will be attained or surpassed this year.

Analysis of effort and catch statistics revealed that the low production in 1957 reflected a severe population decline. This in turn was attributed to the dire effects of intense storm systems which are believed to have compounded expected natural mortality during inshore phases in that year's early-season spawning class. Further analysis eliminated, insofar as available data permitted, the possibility that excessive fishing on spawning stocks or proportionately reduced fishing intensity, rather than poor survival alone, had resulted in the diminished landings.

Trends in overall stock strength were up in the Texas Coast area but gave little hint, despite improved yields, of population recovery in the Louisiana Coast area. Too heavy fishing on dominant early-season spawning classes in 1958 caused postponement of a recovery trend. Relaxed pressure initiated one in 1959. A direct "within-season" relationship between (1) fishing intensity on inshore phases and (2) strength of offshore phases was suggested. Closed inshore seasons first enforced in 1958 were largely ineffectual in bringing about a recovery in that portion of the coastal stock supporting Louisiana's white shrimp fishery.

Other Gulf Populations

Production of white shrimp in Gulf areas other than those already mentioned was negligible during the 4-year study period. A trace was recorded from the Sanibel-Tortugas area (statistical subarea 5) in 1959, and United States fleet landings from the combined East Mexican Coast and Obregon-Campeche areas ranged from less than 0.1 million pounds in 1956 to 0.6 million pounds in 1958 (table 4). As noted earlier, white shrimp taken by United States fishermen comprised only an estimated 1 percent of the total poundage of this species harvested in Mexican waters. Data are too sketchy to permit analyses of white shrimp populations in these areas.

SUMMARY

Those phases of Gulf of Mexico fisheries concerned with the catching, landing, and initial processing of commercial shrimps are briefly described. Knowledge of each species distribution and habits, manner of capture, handling, etc., is reviewed in an attempt to ensure proper interpretation of production statistics as employed to draw inferences about commercial shrimp populations.

The Bureau of Commercial Fisheries continuous survey of Gulf shrimp fisheries is examined critically as to kind and quality of statistics collected. Sources of inaccuracy in effort and landing statistics are pointed out. Effort data, for example, are incomplete due to an inability to determine the extent of "searching" and nonproductive operations, and biased to varying degree in direction and magnitude because of suspect sample projection techniques. Data of overall commercial landings are quite complete, but those for certain species may be biased since distinction between species is not always uniform around the Gulf. Landings, moreover, do not always represent actual catches, or reflect the composition of available populations. More often than not they result from (1) culling catches dominated by small, nonpremium shrimp, or (2) extensive searching for concentrations of premium-size shrimp. Commercial size-classification statistics thereby suffer because their capacity to depict actual size or age structure of exploited populations is lessened.

With real or potential biases being acknowledged, available statistics for each species are used (1) to derive population density indices and (2) to delineate and trace population spawning classes (broods). Short- and long-term trends in population strength are examined in light of trends in corresponding yield. Untoward fluctuations in yield are explained, where possible, in terms of observed population characteristics and their apparent relation to changes in environment and intensity of exploitation.

Commercial statistics reveal that over the period 1956–59, the Gulf of Mexico annually yielded between 167 and 193 million pounds of shrimp to United States fishermen. This represented an average yearly expenditure of 169,000 days' trawling time. About three-fourths of both total effort and yield, respectively, was expended in and taken from waters along the United States coast. Inshore landings and corresponding effort averaged about 21 and 28 percent, respectively, of United States totals. Although overall landings varied mildly during the 4-year study period, those for certain species and in certain areas fluctuated sharply, with fishing success in 1957 having been generally poor.

Of the three major commercial species supporting Gulf of Mexico shrimp fisheries, brown shrimp were the most important, contributing, on the average, 56 percent of annual harvests. Greatest production consistently came from offshore and inshore waters along the northwestern Gulf coast, with Texas waters recognized as this species center of abundance. Over the period 1956–59, brown shrimp population levels rose in the Apalachicola, Pensacola-Mississippi River, and Louisiana Coast areas, remained steady or fell only slightly in the Texas Coast area, and fell perceptibly in the East Mexican Coast area. Corresponding yield trends either remained steady or rose in all areas. Immediate consequences of increasing fishing intensity on declining populations in the Texas and East Mexican Coast areas are problematical.

Serial alignment of monthly weight-frequency curves derived from catch-by-size statistics gave a crude picture of age structure in Gulf of Mexico brown shrimp stocks. Progression of modes inferred two periods of heightened spawning activity each year—one in late winter or early spring, the other in late summer or early fall. Relative strengths of these spawning classes (or broods) obviously varied between as well as within years, but, on the average, early-season classes appeared to be the dominant ones. Superposition of

seasonal spawning and temperature patterns suggested that increased spawning activity was more closely related to temperature reversals than to some fixed or optimum spawning temperature.

Contributing an average of but 22 percent yearly to Gulf of Mexico shrimp landings, pink shrimp ranked second to brown shrimp. Although of relatively minor status on a Gulfwide basis, the species does contribute significantly to the local economy in certain areas. Indeed, since it is the only species of commercial importance occurring off south Florida, the pink shrimp constitutes the sole support of the valuable Sanibel-Tortugas fishery. Practically all Gulf of Mexico pink shrimp production originates in the Sanibel-Tortugas and Gulf of Campeche areas.

Semiannual periods of increased spawning activity also characterize the Sanibel-Tortugas pink shrimp stock. During the period covered by available statistics, relative strengths of early-season and late-season broods appeared roughly equivalent.

From 1956 through 1959, commercial yields of pink shrimp from the Sanibel-Tortugas area suffered a gradual decline. This reflected a downward trend in stock biomass which developed despite a nearly constant (annual) fishing intensity. Whether the effects of too high a sustained, overall fishing intensity were just beginning to manifest themselves during the study period could not be verified due to the lack of prior effort data. The likelihood of excessive fishing being the primary causative factor is considered remote, however, and diminishing population levels are thought to be more a result of greater utilization of small shrimp. Increasingly heavy exploitation of new recruits as they enter the fishery and before their average growth rate reaches a maximum appears to have systematically reduced annual available biomass.

Annual pink shrimp landings from the Gulf of Campeche also experienced a significant downward trend over the period 1956–59. But due to the Campeche fishery's highly selective nature and, consequently, the limited utility of resulting statistics, detailed appraisal of the underlying population was not attempted.

Closely approaching pink shrimp from a production standpoint, white shrimp ranked third in importance to the Gulf of Mexico shrimp industry, comprising about 20 percent of annual shrimp landings. Practically all of this species came from northern Gulf waters with the Louisiana Coast area each year contributing roughly 72 percent of United States Gulf coast totals.

Analyses of monthly size composition data indicated protracted spawning in white shrimp stocks with heightened activity occurring at the beginning and close of each spawning season, April–December. Relative strengths of corresponding spawning classes differed from year to year while early-season classes appeared consistently superior to late-season classes. Average growth compared with that of brown and pink shrimp but varied between early- and late-season classes, and among corresponding classes in different years. Attainment of commercial size is prolonged in late-season classes due to slowed growth during winter months.

Over the period 1956–59, annual white shrimp yields remained relatively stable in the Apalachicola area and rose in the Texas Coast area. Population trends were slightly up in both areas. In contrast, white shrimp fisheries in the Pensacola-Mississippi River and Louisiana Coast areas experienced a severe setback in 1957. Recovery has been fairly rapid in both areas with 1959 landings approaching 1956 levels. But, while white shrimp biomass displayed an upward trend during 1958–59 in the Pensacola-Mississippi River area, population recovery in the Louisiana Coast area lagged perceptibly.

The sharp decline of important white shrimp fisheries in 1957 is largely attributed to factors associated with intense storm systems which are believed to have compounded expected natural mortality during inshore phases of that year's early-season spawning class. Too heavy fishing on the dominant early-season spawning class in 1958 is postulated as having postponed a population recovery trend in the Louisiana Coast area. Relaxed pressure seemingly initiated one in 1959. Closed inshore seasons first enforced in 1958 cannot be credited with having expedited recovery since they mainly include periods during which fishable white shrimp normally exhibit minimal density. White shrimp population strength appears primarily governed by the environment, but excessive fishing intensity too soon after a catastrophic ebb may stifle quick recovery.

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APPENDIX

TABLE A1.—*Effort expended by the United States commercial shrimp fleet in the Gulf of Mexico, 1956–59*

[24-hour units' trawling]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
SANIBEL-TORTUGAS													
1956													
Inshore													
0–10	2.5	110.9	235.6	229.6	230.1	17.6	6.1			1.2	5.0	11.2	849.8
11–20	1,485.4	1,931.0	2,210.5	2,177.9	2,234.2	1,134.2	380.3	442.9	191.6	495.9	921.8	1,834.4	15,440.1
21–45	318.2	262.6	79.0	254.5	204.3	23.3	3.6	5.8	2.5		3.8	71.5	1,229.1
Offshore	1,806.1	2,304.5	2,525.1	2,662.0	2,668.6	1,175.1	390.0	448.7	194.1	497.1	930.6	1,917.1	17,519.0
1957													
Inshore													
0–10	69.5	126.5	148.4	153.3	97.1	29.9	1.6			.4	21.1	2.5	650.3
11–20	2,816.4	2,400.7	2,755.4	1,608.7	1,447.1	740.7	415.7	252.7	306.7	495.6	1,373.8	1,405.2	16,018.7
21–45	61.0	68.8	154.9	81.8	28.9	35.1	11.7	20.2	6.0	12.3	67.6	118.6	666.9
Offshore	2,946.9	2,596.0	3,058.7	1,843.8	1,573.1	805.7	429.0	272.9	312.7	508.3	1,462.5	1,526.3	17,335.9
1958													
Inshore													
0–10	16.5	278.0	499.4	794.3	467.5	174.4	50.2	1.7	3.0	.1	73.2	130.1	2,488.4
11–20	2,272.3	1,972.1	2,341.1	2,211.7	2,000.7	877.6	320.9	508.8	639.5	764.6	1,523.4	1,355.0	16,787.7
21–45	176.1	257.9	241.6	88.6	97.6	3.0	4.6	189.8	45.8	3.7	72.4	232.7	1,413.8
Offshore	2,464.9	2,508.0	3,082.1	3,094.6	2,565.8	1,055.0	375.7	700.3	688.3	768.4	1,669.0	1,717.8	20,689.9
1959													
Inshore													
0–10	223.3	324.9	398.2	509.5	321.9	160.8	39.8	21.0	15.2	12.0	60.3	53.9	2,140.8
11–20	2,363.6	1,963.9	2,136.6	1,341.5	1,288.7	671.9	190.9	136.3	149.4	330.6	535.6	1,481.2	12,590.2
21–45	523.1	891.4	322.5	307.0	115.5	140.7	12.6				4.8	44.3	2,366.9
Offshore	3,110.0	3,180.2	2,857.3	2,158.0	1,726.1	973.4	243.3	157.3	164.6	342.6	600.7	1,584.4	17,097.9
APALACHICOLA													
1956													
Inshore	12.5	1.5	85.2	123.0	328.7	123.6	60.2	119.6	175.9	306.9	296.7	58.8	1,692.6
0–10	23.3	3.5	3.8	183.7	566.2	213.7	204.9	4.0	.4	148.0	125.9	176.3	1,653.7
11–20	8.0	.5			225.4	237.9	38.9	15.0	83.1				608.8
21–45													
Offshore	31.3	4.0	3.8	183.7	791.6	451.6	243.8	19.0	83.5	148.0	125.9	176.3	2,262.5
1957													
Inshore	40.6	26.5	112.2	352.5	420.9	185.8	248.5	172.5	480.0	250.4	257.5	54.0	2,601.4
0–10	107.8	93.6	117.1	79.3	207.3	44.0	42.0	11.0	17.3	87.0	122.8	248.9	1,178.1
11–20				200.5	28.3	120.7	114.0	7.5	1.0	59.0	27.7	2.5	561.2
21–45													
Offshore	107.8	93.6	117.1	279.8	235.6	164.7	156.0	18.5	18.3	146.0	150.5	251.4	1,739.3
1958													
Inshore			13.0	82.9	286.9	241.8	607.0	276.7	543.1	315.9	104.8	92.2	2,564.3
0–10	62.8	8.0	36.3	124.2	510.7	281.9	146.1	67.2	8.9	99.3	57.5	155.4	1,558.3
11–20				.4	46.8	17.7	19.0	8.5		1.0	20.5	14.3	128.2
21–45													
Offshore	62.8	8.0	36.3	124.6	557.5	299.6	165.1	75.7	8.9	100.3	78.0	169.7	1,686.5
1959													
Inshore	2.5	17.4	94.4	254.8	348.9	231.0	167.8	130.0	170.1	255.5	103.2	24.0	1,799.6
0–10	81.9	16.9	12.9	262.2	385.7	105.3	50.9	14.5	53.6	75.4	131.5	113.8	1,[illegible]
11–20	1.0				6.9	46.5	17.5	5.5					[illegible]
21–45													
Offshore	82.9	16.9	12.9	262.2	392.6	151.8	68.4	20.0	53.6	75.4	131.5	113.8	1,[illegible]

TABLE A1.—*Effort expended by the United States commercial shrimp fleet in the Gulf of Mexico, 1956–59*—Continued

[24-hour units' trawling]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
PENSACOLA-MISSISSIPPI RIVER													
1956													
Inshore	27.5	2.7	10.8	66.2	432.7	2,110.1	1,917.5	2,682.0	1,878.6	1,905.9	1,547.7	199.1	12,780.8
0–10	17.3	9.0	.5	4.0	48.3	1,455.4	1,643.0	907.3	170.4	393.0	538.1	152.1	5,338.4
11–20	43.5	27.0	----	39.8	194.2	886.1	1,363.0	688.9	369.6	287.8	216.7	204.3	4,220.9
21–45	334.8	325.0	405.0	351.6	323.1	112.6	15.0	438.5	252.6	300.4	82.9	270.8	3,212.3
Offshore	395.6	361.0	405.5	395.4	565.6	2,454.1	3,021.0	2,034.7	792.6	981.2	837.7	627.2	12,871.6
1957													
Inshore	23.8	12.2	58.3	157.3	930.6	1,881.1	1,796.3	2,429.2	2,365.2	982.4	1,077.3	956.1	12,669.8
0–10	23.5	4.5	1.0	1.7	176.3	1,587.4	1,452.5	555.9	65.0	63.3	64.3	20.8	4,016.2
11–20	92.4	14.3	8.3	----	181.1	640.7	826.7	1,014.5	365.7	283.3	245.9	225.3	3,898.2
21–45	124.1	153.6	48.3	34.7	236.7	25.5	----	574.4	602.8	284.8	140.9	120.4	2,346.2
Offshore	240.0	172.4	57.6	36.4	594.1	2,253.6	2,279.2	2,144.8	1,033.5	631.4	451.1	366.5	10,260.6
1958													
Inshore	49.6	10.0	18.0	168.6	153.0	1,866.3	1,791.4	2,867.7	1,810.9	2,313.0	1,195.5	286.3	12,530.3
0–10	2.0	2.5	2.0	8.2	10.4	571.2	1,024.6	518.5	62.8	131.2	220.0	97.2	2,650.6
11–20	26.6	72.9	12.1	8.4	14.4	152.6	886.7	845.9	306.0	165.3	143.9	230.7	2,865.5
21–45	142.5	122.2	196.3	116.7	11.3	54.1	13.2	195.2	192.3	101.8	144.7	134.9	1,425.2
Offshore	171.1	197.6	210.4	133.3	36.1	777.9	1,924.5	1,559.6	561.1	398.3	508.6	462.8	6,941.3
1959													
Inshore	23.3	----	1.6	42.3	174.9	2,997.8	2,234.4	2,425.5	4,344.7	1,940.5	1,249.7	112.5	15,547.2
0–10	26.0	20.3	1.0	2.1	24.7	1,279.4	740.2	605.4	175.9	301.1	301.5	94.4	3,572.0
11–20	83.5	15.3	5.5	4.2	81.0	827.9	1,766.6	1,047.2	484.2	135.6	283.3	182.0	4,916.3
21–45	91.3	16.0	13.5	6.9	11.4	----	343.0	212.4	143.4	119.4	133.6	75.6	1,166.5
Offshore	200.8	51.6	20.0	13.2	117.1	2,107.3	2,849.8	1,865.0	803.5	556.1	718.4	352.0	9,654.8
LOUISIANA COAST													
1956													
Inshore	107.3	6.0	6.0	21.5	4,234.2	1,999.7	86.8	1,942.3	2,344.5	2,567.3	1,709.5	675.5	15,700.6
0–10	829.2	500.1	481.6	438.3	1,813.7	1,222.5	586.7	892.2	1,664.7	3,213.5	2,590.3	1,880.3	16,113.1
11–20	76.3	130.1	312.1	350.1	284.7	836.0	2,257.0	2,839.6	533.7	921.7	658.8	456.6	9,656.7
21–45	621.2	392.3	732.3	976.8	879.2	35.2	258.9	15.7	60.5	282.3	68.1	133.1	4,455.6
Offshore	1,526.7	1,022.5	1,526.0	1,765.2	2,977.6	2,093.7	3,102.6	3,747.5	2,258.9	4,417.5	3,317.2	2,470.0	30,225.4
1957													
Inshore	6.0	----	1.5	667.2	3,079.4	2,599.3	512.0	1,621.4	2,136.0	1,807.2	420.9	261.5	13,112.4
0–10	861.0	747.1	446.6	587.4	1,287.6	1,330.1	114.0	699.0	1,255.8	2,672.1	1,398.8	833.4	12,232.9
11–20	451.3	346.7	127.3	196.0	516.7	475.5	952.4	698.0	428.7	161.0	54.4	231.4	4,639.4
21–45	142.3	258.4	185.2	180.5	87.1	.7	4.5	141.5	7.0	37.7	37.7	148.1	1,230.7
Offshore	1,454.6	1,352.2	759.1	963.9	1,891.4	1,806.3	1,070.9	1,538.5	1,691.5	2,870.8	1,490.9	1,212.9	18,103.
1958													
Inshore	182.1	----	178.7	9.0	1,340.0	5,552.2	38.0	2,984.1	2,382.5	4,413.6	2,990.4	138.8	20,209.4
0–10	306.8	179.6	257.8	603.4	1,174.9	1,895.9	349.0	2,129.1	3,038.9	3,539.3	3,715.7	3,425.6	20,616.0
11–20	189.4	276.4	198.2	112.0	402.5	306.4	1,538.5	2,656.1	854.7	48.9	58.7	189.9	6,831.7
21–45	517.2	107.4	373.0	643.9	555.8	127.6	794.0	701.4	334.6	412.0	213.6	326.1	5,106.6
Offshore	1,013.4	563.4	829.0	1,359.3	2,133.2	2,329.9	2,681.5	5,486.6	4,228.2	4,000.2	3,988.0	3,941.6	32,554.3
1959													
Inshore	----	----	----	----	4,036.0	5,814.0	1.0	2,831.4	4,591.5	3,585.0	467.3	79.6	21,405.8
0–10	391.8	46.8	84.9	478.2	1,613.9	1,755.2	192.8	1,315.4	1,736.4	4,748.0	4,284.6	1,938.6	18,586.6
11–20	399.7	173.1	211.2	288.7	887.7	1,118.9	2,854.8	1,141.8	889.7	303.8	222.2	521.8	9,013.4
21–45	600.6	562.7	555.6	1,056.1	790.1	123.4	146.3	166.2	109.8	175.1	78.5	404.5	4,768.9
Offshore	1,392.1	782.6	851.7	1,823.0	3,291.7	2,997.5	3,193.9	2,623.4	2,735.9	5,226.9	4,585.3	2,864.9	32,368.9

TABLE A1.—*Effort expended by the United States commercial shrimp fleet in the Gulf of Mexico, 1956–59*—Continued

[24-hour units' trawling]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
TEXAS COAST													
1956													
Inshore	.5		5.4	153.7	320.2	75.7	2.0		652.8	725.5	331.9		2,267.7
0–10	.4	8.1	114.5	111.8	965.7	354.3	247.1	57.7	468.2	478.6	290.9	59.8	3,157.1
11–20	161.4	63.2	39.2	624.5	844.2	950.0	3,235.3	5,801.9	3,576.4	3,627.2	1,497.3	732.9	21,153.5
21–45	893.6	593.0	834.6	494.4	255.4	388.5	185.5	431.7	1,125.3	710.3	822.8	756.0	7,491.1
Offshore	1,055.4	664.3	988.3	1,230.7	2,065.3	1,692.8	3,667.9	6,291.3	5,169.9	4,816.1	2,611.0	1,548.7	31,801.7
1957													
Inshore				22.0	858.3	401.0		104.5	1,597.6	884.9	58.7		3,927.0
0–10	1.6	1.8	10.1	35.9	55.1	60.9	80.9	208.8	190.8	185.4	203.4	51.4	1,086.1
11–20	154.4	41.6	210.5	221.0	590.7	3,002.4	5,916.0	5,602.0	3,785.3	3,280.6	1,791.2	465.8	25,061.5
21–45	929.3	1,386.4	922.6	667.1	580.3	264.8	19.3	281.2	370.6	290.8	809.2	1,030.1	7,551.7
Offshore	1,085.3	1,429.8	1,143.2	924.0	1,226.1	3,328.1	6,016.2	6,092.0	4,346.7	3,756.8	2,803.8	1,547.3	33,699.3
1958													
Inshore				52.0	284.9	343.8	70.4	466.9	1,951.5	932.7	546.2	78.3	4,726.7
0–10	.5		57.2	441.5	311.9	552.6	559.3	570.0	1,179.5	1,377.8	765.9	1,111.4	6,927.6
11–20	309.3	42.5	26.6	354.0	1,568.8	3,395.6	6,525.8	7,285.3	5,854.7	2,787.3	978.0	854.1	29,982.0
21–45	835.1	763.3	802.4	552.2	266.0	424.2	206.5	8.9	90.2	244.6	383.2	372.9	4,949.5
Offshore	1,144.9	805.8	886.2	1,347.7	2,146.7	4,372.4	7,291.6	7,864.2	7,124.4	4,409.7	2,127.1	2,338.4	41,859.1
1959													
Inshore				14.2	95.7	33.1	66.5	643.6	1,287.7	1,831.3	157.3	28.3	4,157.7
0–10	139.9	11.3	34.4	200.9	432.8	33.2	111.8	254.3	668.4	962.3	775.9	127.9	3,753.1
11–20	245.6	140.1	172.2	211.3	1,136.8	1,087.0	3,506.7	5,638.7	5,940.0	4,550.3	1,577.0	1,050.2	25,255.9
21–45	422.1	374.4	582.7	329.9	236.4	83.8	458.7	995.7	736.6	757.4	500.8	570.2	6,048.7
Offshore	807.6	525.8	789.3	742.1	1,806.0	1,204.0	4,077.2	6,888.7	7,345.0	6,270.0	2,853.7	1,748.3	35,057.7
EAST MEXICAN COAST													
1956													
Inshore													
0–10				2.7	2.7		2.7	6.0					14.1
11–20	27.8	167.2	32.7	128.3	156.4	149.7	144.1	128.1	240.2	259.8	354.0	151.4	1,939.7
21–45	1,397.2	945.2	1,157.7	881.1	843.2	1,149.7	744.5	570.5	740.8	1,639.3	1,005.3	1,347.1	12,421.6
Offshore	1,425.0	1,112.4	1,190.4	1,012.1	1,002.3	1,299.4	891.3	704.6	981.0	1,899.1	1,359.3	1,498.5	14,375.4
1957													
Inshore													
0–10	1.7	1.9	5.7	4.7	7.6	8.5	5.9	1.6	.2				37.8
11–20	74.0	39.3	121.7	111.0	138.1	193.1	843.5	769.8	542.5	279.7	478.6	472.4	4,063.7
21–45	1,017.0	974.9	1,041.2	925.6	1,593.1	1,463.8	1,053.6	672.7	1,194.8	1,426.9	1,162.2	999.7	13,525.5
Offshore	1,092.7	1,016.1	1,168.6	1,041.3	1,738.8	1,665.4	1,903.0	1,441.1	1,737.5	1,706.6	1,640.8	1,472.1	17,627.0
1958													
Inshore													
0–10											83.6	185.7	269.3
11–20	263.1	117.5	97.7	119.5	129.7	238.5	151.0	7.1	68.4	634.9	463.8	552.1	2,843.3
21–45	2,163.0	1,995.1	2,868.3	2,554.1	2,965.9	1,313.2	275.0	111.1	214.7	2,475.5	2,344.3	1,798.8	21,079.0
Offshore	2,426.1	2,112.6	2,966.0	2,673.6	3,095.6	1,551.7	426.0	118.2	283.1	3,110.4	2,891.7	2,536.6	24,191.6
1959													
Inshore													
0–10	39.3	16.3	11.7	40.1	107.7	54.3	.4						269.8
11–20	170.6	106.7	393.2	193.5	191.7	408.5	294.4	407.4	287.4	418.8	191.4	305.8	3,369.4
21–45	1,425.1	1,679.9	1,505.4	1,306.7	727.3	747.2	356.9	853.8	1,299.5	1,443.4	1,155.0	1,431.9	13,972.1
Offshore	1,635.0	1,802.9	1,910.3	1,540.3	1,026.7	1,210.0	651.7	1,261.2	1,586.9	1,862.2	1,386.4	1,737.7	17,613.3

TABLE A1.—*Effort expended by the United States commercial shrimp fleet in the Gulf of Mexico, 1956–1959*—Continued

[24-hour units' trawling]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
OBREGON-CAMPECHE													
1956													
Inshore													
0–10	176.0	203.0	313.0	153.5	201.5	153.4	58.3	21.3	7.1	19.9	5.5	182.3	1,494.8
11–20	714.7	1,924.5	1,302.3	1,661.9	1,521.1	1,422.0	1,909.3	1,291.7	1,583.8	1,172.3	860.9	2,022.6	17,387.1
21–45	143.8	737.4	590.5	319.3	202.9	81.4	38.7	75.0	36.1	310.7	413.4	404.7	3,353.9
Offshore	1,034.5	2,864.9	2,205.8	2,134.7	1,925.5	1,656.8	2,006.3	1,388.0	1,627.0	1,502.9	1,279.8	2,609.6	22,235.8
1957													
Inshore													
0–10	209.1	570.2	410.0	300.0	157.0	158.5	116.2	103.9	58.8	125.1	25.5	145.1	2,379.4
11–20	447.2	1,655.9	951.5	1,699.0	1,958.6	2,084.6	1,606.9	1,501.4	1,242.2	1,243.4	717.6	1,555.1	16,663.4
21–45	178.0	249.3	176.2	166.1	102.2	183.4	123.9	62.5	112.6	380.7	307.1	405.9	2,447.9
Offshore	834.3	2,475.4	1,537.7	2,165.1	2,217.8	2,426.5	1,847.0	1,667.8	1,413.6	1,749.2	1,050.2	2,106.1	21,490.7
1958													
Inshore													
0–10	104.4	335.9	362.4	338.7	315.0	132.6	95.7	43.3	47.8	49.0	39.1	157.7	2,021.6
11–20	549.8	864.7	1,029.4	1,365.1	1,340.3	1,449.6	1,522.2	967.9	394.6	667.3	434.9	980.6	11,566.4
21–45	187.5	360.1	306.6	432.7	109.2	100.2	155.6	72.1	2.3	97.7	430.2	1,057.0	3,311.2
Offshore	841.7	1,560.7	1,698.4	2,136.5	1,764.5	1,682.4	1,773.5	1,083.3	444.7	814.0	904.2	2,195.3	16,899.2
1959													
Inshore													
0–10	212.0	431.0	561.5	334.6	723.1	251.8	23.5	28.3	31.7	73.8	15.2	388.8	3,075.3
11–20	522.1	1,269.0	1,197.4	1,319.4	1,796.2	1,807.0	2,044.8	518.1	586.9	577.5	411.9	1,576.2	13,626.5
21–45	259.3	509.0	621.9	397.2	380.6	90.8	76.4	8.1	4.4	58.0	214.0	387.6	3,007.3
Offshore	993.4	2,209.0	2,380.8	2,051.2	2,899.9	2,149.6	2,141.7	554.5	623.0	709.3	641.1	2,352.6	19,709.1

TABLE A2.—*Brown shrimp landings by the United States commercial fleet, Gulf of Mexico, 1956–59*

[Thousands of pounds, heads on]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
APALACHICOLA													
1956													
Inshore	3.5	0.4			4.0	6.2	16.5	59.9	46.4	50.4	0.8		188.1
0–10	1.6	.8			7.2		5.8	2.0		20.6			38.0
11–20		.3			15.8	24.9	10.4	7.5					58.9
21–45													
Offshore	1.6	1.1			23.0	24.9	16.2	9.5		20.6			96.9
1957													
Inshore			48.4	11.1	5.2	13.8	125.0	88.5	63.5	43.5	12.1	21.1	432.2
0–10			30.6	43.5	2.0		3.4	9.6					89.1
11–20				29.7		2.6	.3	6.2					38.8
21–45													
Offshore			30.6	73.2	2.0	2.6	3.7	15.8					127.9
1958													
Inshore						115.2	442.3	102.0	39.5	22.5	2.0		723.5
0–10				.3	9.9	88.6	125.2	32.4	.2		1.5		258.1
11–20						1.8	1.5	7.1				.2	10.6
21–45													
Offshore				.3	9.9	90.4	126.7	39.5	.2		1.5	.2	268.7
1959													
Inshore	.1	4.5	29.2	103.2	144.5	100.1	70.6	50.3	24.5	9.6	5.7	2.9	545.1
0–10	.1	.8	3.9	250.3	284.9	52.1	29.2	6.2	6.2		.3		634.0
11–20					2.0	44.2	12.1	3.1					61.4
21–45													
Offshore	.1	.8	3.9	250.3	286.9	96.3	41.3	9.3	6.2		.3		695.4

TABLE A2.—*Brown shrimp landings by the United States commercial fleet, Gulf of Mexico, 1956–59*

[Thousands of pounds, heads on]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
PENSACOLA-MISSISSIPPI RIVER													
1956													
Inshore	.3			2.0	196.6	1,621.9	1,375.6	990.2	163.8	76.4	107.4	39.8	4,574.0
0–10	2.0	.3		3.4	31.8	2,121.7	2,059.3	971.7	62.2	11.8	49.4	6.2	5,319.8
11–20	4.0	3.5		18.0	34.6	979.1	1,324.5	667.3	415.3	358.5	106.7	126.2	4,037.7
21–45	179.3	119.3	185.0	175.2	148.7	245.8	6.4	411.4	292.3	389.5	76.6	234.5	2,464.0
Offshore	185.3	123.1	185.0	196.6	215.1	3,346.6	3,390.2	2,050.4	769.8	759.8	232.7	366.9	11,821.5
1957													
Inshore	11.8	2.2	5.9	25.5	215.4	1,468.7	1,219.7	991.9	345.1	132.7	153.2	175.1	4,747.2
0–10	1.3		.5	.3	83.5	2,180.3	1,807.0	518.6	24.5	10.9	11.4	7.7	4,646.0
11–20	50.4	2.5	2.0		61.0	467.2	988.8	1,118.4	406.7	295.3	171.5	113.6	3,677.4
21–45	95.4	109.4	27.4	19.8	127.3	18.1		580.4	715.7	316.3	120.1	84.2	2,214.1
Offshore	147.1	111.9	29.9	20.1	271.8	2,665.6	2,795.8	2,217.4	1,146.9	622.5	303.0	205.5	10,537.5
1958													
Inshore	10.4	2.8	7.4	18.3	23.0	1,059.4	1,177.5	894.6	233.2	45.7	9.4	4.4	3,486.1
0–10	1.7	.8	1.3	1.0	.8	597.6	1,072.5	459.8	33.6	9.6	1.5	2.9	2,183.1
11–20	15.1	30.2	7.9	3.7	7.6	103.8	825.7	836.5	270.6	73.1	25.7	13.4	2,213.3
21–45	109.2	93.1	152.0	79.8	6.0	30.4	13.8	146.5	146.5	36.5	17.0	80.1	910.9
Offshore	126.0	124.1	161.2	84.5	14.4	731.8	1,912.0	1,442.8	450.7	119.2	44.2	96.4	5,307.3
1959													
Inshore	1.0				21.0	3,668.4	2,080.8	536.8	120.8	43.5	16.8	8.9	6,498.0
0–10	6.6			.2	3.7	2,634.6	1,073.7	677.2	50.4	43.3	36.0	13.8	4,539.5
11–20	8.4	5.0	4.9	1.1	33.9	1,388.9	2,912.3	1,439.9	607.3	98.8	110.4	150.7	6,761.6
21–45	37.0	11.8	4.5	2.4	6.2		519.1	262.2	197.4	128.4	91.1	44.6	1,304.7
Offshore	52.0	16.8	9.4	3.7	43.8	4,023.5	4,505.1	2,379.3	855.1	270.5	237.5	209.1	12,605.8
LOUISIANA COAST													
1956													
Inshore					4,243.2	3,493.1	55.9	5.9					7,798.1
0–10	8.4	9.4	5.2	6.2	640.2	288.3	212.9	137.9	65.2	30.2	22.5	42.5	1,468.9
11–20	9.2	3.2	14.3	91.6	82.2	740.2	3,032.6	3,452.7	527.7	522.0	153.7	400.2	9,029.6
21–45	461.5	250.5	409.6	510.9	356.0	18.5	303.2	13.4	62.7	387.9	70.1	104.5	2,948.8
Offshore	479.1	263.1	429.1	608.7	1,078.4	1,047.0	3,548.7	3,604.0	655.6	940.1	246.3	547.2	13,447.3
1957													
Inshore					513.1	4,532.1	3,672.3	666.6	656.0	316.8			10,356.9
0–10	20.8	11.8	5.2	66.7	318.2	457.3	134.6	298.2	593.0	168.0	55.1	19.8	2,148.7
11–20	307.6	246.8	48.4	21.7	254.5	547.2	1,478.2	996.9	656.5	295.3	115.9	163.6	5,132.6
21–45	112.2	160.4	92.2	61.0	49.4	1.2	11.8	254.9	10.6	43.7	41.3	95.8	934.5
Offshore	440.6	419.0	145.8	149.4	622.1	1,005.7	1,624.6	1,550.0	1,260.1	507.0	212.3	279.2	8,215.8
1958													
Inshore	36.6		64.3	6.5	612.9	3,365.4	20.8	241.4	340.4	1.0	3.7		4,693.0
0–10	15.8	2.1	.5	2.0	152.2	518.3	24.4	253.2	38.5	6.0	43.2	55.8	1,112.0
11–20	21.2	147.0	138.6	74.7	242.3	284.6	1,557.7	4,060.1	1,265.2	31.1	31.2	191.0	8,044.7
21–45	158.1	78.5	235.2	496.1	427.1	95.3	523.0	19.8	101.0	126.5	161.4	153.2	2,575.2
Offshore	195.1	227.6	374.3	572.8	821.6	898.2	2,105.1	4,333.1	1,404.7	163.6	235.8	400.0	11,731.9
1959													
Inshore					4,134.6	6,794.9	1.5	9.2					10,940.2
0–10	5.4	4.9	.8		427.7	597.3	138.8	37.8	16.5	34.8	24.9	12.2	1,301.1
11–20	290.3	128.9	191.4	258.2	326.1	1,401.8	5,884.7	1,770.4	868.7	400.5	185.8	476.7	12,183.5
21–45	215.0	283.4	276.7	716.0	439.0	45.4	196.4	188.7	128.4	177.9	54.8	114.0	2,835.7
Offshore	510.7	417.2	468.9	974.2	1,192.8	2,044.5	6,219.9	1,996.9	1,013.6	613.2	265.5	602.9	16,320.3
TEXAS COAST													
1956													
Inshore				57.0	122.6	96.9	4.9			49.2			330.6
0–10			5.7	3.2	9.9	102.3	152.9	36.0	23.0	6.0	5.5	4.2	348.7
11–20	99.6	37.3	14.1	360.7	306.8	610.5	4,765.3	8,097.8	5,170.9	5,677.2	2,043.9	1,011.7	28,195.8
21–45	808.7	438.3	586.8	372.8	166.5	250.2	205.6	611.4	1,735.9	1,128.3	1,135.8	1,003.5	8,443.8
Offshore	908.3	475.6	606.6	736.7	483.2	963.0	5,123.8	8,745.2	6,929.8	6,811.5	3,185.2	2,019.4	36,988.3
1957													
Inshore				1.3	1,547.6	630.0		3.4	1.3	34.8			2,218.4
0–10	1.0	1.8	3.9	.7	2.4	9.4	69.0	215.5	33.9	13.4	18.0	3	[illegible]
11–20	204.1	97.6	185.5	186.0	406.6	3,251.3	8,335.2	8,600.3	6,368.2	6,771.1	2,973.1	491.7	[illegible]
21–45	1,227.2	1,536.4	857.0	612.9	401.5	175.9	27.6	398.8	533.4	473.9	1,089.9	1,205.1	8,549.6
Offshore	1,432.3	1,635.8	1,046.4	799.6	810.5	3,436.6	8,431.8	9,214.6	6,935.5	7,258.4	4,091.0	1,697.1	46,789.6

TABLE A2.—*Brown shrimp landings by the United States commercial fleet, Gulf of Mexico, 1956-59*—Continued

[Thousands of pounds, heads on]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
TEXAS COAST—continued													
1958													
Inshore				18.6	128.7	366.1	.8		.7		.7	.5	516.1
0–10	.2		.2	29.2	71.7	243.9	809.3	325.9	95.6	27.4	7.9	9.7	1,621.0
11–20	274.0	29.2	13.3	174.6	861.7	3,176.2	8,520.3	7,346.3	8,348.8	3,809.7	1,204.7	619.0	34,377.8
21–45	767.1	533.9	547.5	301.9	132.0	254.9	158.3	7.4	149.7	374.5	446.4	288.5	3,962.1
Offshore	1,041.3	563.1	561.0	505.7	1,065.4	3,675.0	9,487.9	7,679.6	8,594.1	4,211.6	1,659.0	917.2	39,960.9
1959													
Inshore					6.6	57.5	114.1	24.0	6.7			3.0	211.9
0–10	.5	0.3	.5	2.7	7.7	2.9	131.9	253.8	83.2	75.4	25.2	6.5	590.6
11–20	110.7	52.8	50.9	56.3	362.4	531.0	7,502.0	10,723.4	10,654.1	8,088.9	1,854.9	922.8	40,910.2
21–45	245.1	147.0	273.0	118.3	106.2	38.1	944.7	1,945.3	1,313.8	1,420.9	660.1	639.3	7,851.8
Offshore	356.3	200.1	324.4	177.3	476.3	572.0	8,578.6	12,922.5	12,051.1	9,585.2	2,540.2	1,568.6	49,352.6
EAST MEXICAN COAST													
1956													
Inshore													
0–10				2.7			1.7	8.4					12.8
11–20	32.9	129.0	27.9	104.1	109.8	113.6	134.1	156.9	369.3	460.7	357.5	228.2	2,224.0
21–45	1,310.5	826.9	963.6	759.9	674.6	915.2	706.9	642.4	1,117.5	2,668.2	1,438.6	2,112.9	14,137.2
Offshore	1,343.4	955.9	991.5	866.7	784.4	1,028.8	842.7	807.7	1,486.8	3,128.9	1,796.1	2,341.1	16,374.0
1957													
Inshore													
0–10	1.3	1.5	3.4	2.3	3.0	6.9	7.6	1.8	.2				28.0
11–20	114.9	59.9	127.1	112.6	103.0	185.8	1,325.1	1,018.8	776.3	479.1	723.4	512.4	5,538.4
21–45	1,626.7	1,557.4	1,222.0	1,128.8	1,290.9	1,224.4	1,579.3	953.2	1,874.3	2,925.2	1,706.4	1,105.2	18,193.8
Offshore	1,742.9	1,618.8	1,352.5	1,243.7	1,396.9	1,417.1	2,912.0	1,973.8	2,650.8	3,404.3	2,429.8	1,617.6	23,760.2
1958													
Inshore													
0–10											4.2	1.8	6.0
11–20	232.2	122.8	68.9	67.4	44.2	150.9	146.6	7.7	111.5	775.1	363.9	306.2	2,397.4
21–45	1,815.6	1,498.2	1,787.4	1,304.0	1,341.4	706.3	214.6	86.9	364.2	3,295.2	2,516.8	1,089.0	16,019.6
Offshore	2,047.8	1,621.0	1,856.3	1,371.4	1,385.6	857.2	361.2	94.6	475.7	4,070.3	2,884.9	1,397.0	18,423.0
1959													
Inshore													
0–10		4.3		.2	4.2		.5						9.2
11–20	75.8	49.7	164.6	73.9	75.5	617.9	612.7	808.6	594.2	542.4	184.6	218.3	4,018.2
21–45	814.0	1,106.5	691.0	621.2	345.4	494.6	550.5	1,787.2	2,734.2	2,141.1	1,590.9	1,607.0	14,483.6
Offshore	889.8	1,160.5	855.6	695.3	425.1	1,112.5	1,163.7	2,595.8	3,328.4	2,683.5	1,775.5	1,825.3	18,511.0
ORREGON-CAMPECHE													
1956													
Inshore													
0–10													
11–20		4.5	13.9	36.6	4.2	2.7	19.5	26.8	70.1	13.9	15.5	6.2	213.9
21–45	37.8	82.6	112.7	21.5		21.8	12.7	94.5	40.4	84.7	2.5	26.0	537.2
Offshore	37.8	87.1	126.6	58.1	4.2	24.5	32.2	121.3	110.5	98.6	18.0	32.2	751.1
1957													
Inshore													
0–10													
11–20	5.2	30.6	8.1	11.4	15.8	14.6	.5	1.7	25.5	6.2	11.6	1.8	133.0
21–45	3.9	18.0	35.4	40.8	22.2	29.1	5.7	2.0	31.8	69.2	7.1		265.2
Offshore	9.1	48.6	43.5	52.2	38.0	43.7	6.2	3.7	57.3	75.4	18.7	1.8	398.2
1958													
Inshore													
0–10						1.0	1.3						2.3
11–20		3.2	12.8	26.7	59.1	99.9	125.0	11.1	10.8	2.9	1.5	39.5	392.5
21–45		38.0	61.2	80.1	22.8	57.1	91.1	37.2		21.0	2.5	9.7	420.7
Offshore		41.2	74.0	106.8	81.9	158.0	217.4	48.3	10.8	23.9	4.0	49.2	815.5
1959													
Inshore													
0–10	2.5	1.2	2.4	.2	.5	34.9						.2	41.9
11–20	31.1	99.0	131.4	98.0	225.1	217.6	84.7				37.8	62.6	987.3
21–45	61.3	104.8	209.3	59.4	54.5	8.4	9.9		9.2	13.6	1.0		531.4
Offshore	94.9	205.0	343.1	157.6	280.1	260.9	94.6		9.2	13.6	38.8	62.8	1,560.6

TABLE A3.—*Pink shrimp landings* [1] *by the United States commercial fleet, Gulf of Mexico, 1956–59*

[Thousands of pounds, heads on]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
SANIBEL-TORTUGAS													
1956													
Inshore													
0–10	1.3	98.9	239.1	169.5	159.0	7.6	3.7			13.3	5.7	8.9	707.0
11–20	1,834.4	2,124.2	2,634.1	2,390.7	2,088.4	1,381.7	441.5	393.3	241.6	1,550.1	2,008.1	2,396.2	19,487.3
21–45	450.2	224.8	63.3	213.2	134.9	15.9	4.2	2.3	.8		7.6	81.1	1,198.3
Offshore	2,285.9	2,447.9	2,936.5	2,773.4	2,382.3	1,405.2	449.4	395.6	245.4	1,563.4	2,021.4	2,486.2	21,392.6
1957													
Inshore													
0–10	49.4	71.9	91.1	94.1	52.6	21.1	.8			.5	21.5	3.3	406.3
11–20	3,210.3	1,815.4	2,502.6	1,349.4	1,461.6	622.5	473.7	181.4	371.3	573.6	1,507.1	1,691.7	15,760.6
21–45	55.6	37.4	98.8	39.1	18.0	15.5	7.6	11.8	6.9	13.3	80.8	137.1	521.9
Offshore	3,315.3	1,924.7	2,692.5	1,482.6	1,532.2	659.1	482.1	193.2	378.2	578.4	1,609.4	1,832.1	16,688.8
1958													
Inshore													
0–10	22.0	329.3	842.2	1,106.8	858.1	185.8	63.8	2.0	3.0		86.3	103.0	3,602.3
11–20	2,771.2	1,635.3	2,397.9	3,024.5	2,478.0	1,278.2	380.5	714.0	990.2	1,071.0	1,906.6	1,191.1	19,838.5
21–45	185.1	197.4	145.4	78.4	67.1	1.2	6.5	237.7	36.8	3.7	91.4	207.3	1,258.0
Offshore	2,978.3	2,162.0	3,385.5	4,209.7	3,403.2	1,465.2	450.8	953.7	1,030.0	1,074.7	2,084.3	1,501.4	24,698.8
1959													
Inshore													
0–10	163.6	235.8	202.4	273.5	161.9	86.2	32.8	23.2	12.3	12.8	85.0	46.4	1,335.9
11–20	1,914.7	1,096.6	1,273.4	926.1	1,130.5	432.6	138.4	88.4	167.8	551.9	1,045.0	2,406.1	11,171.5
21–45	402.3	477.5	154.5	178.1	52.0	60.7	5.9				6.9	69.4	1,407.3
Offshore	2,480.6	1,809.9	1,630.3	1,377.7	1,344.4	579.5	177.1	111.6	180.1	564.7	1,136.9	2,521.9	13,914.7
APALACHICOLA													
1956													
Inshore			31.1	66.5	128.2	61.8	12.9	5.0	6.9	3.0	33.8	25.4	374.6
0–10			1.0	100.0	349.2	263.9	118.3						832.4
11–20					113.4		17.3						130.7
21–45													
Offshore			1.0	100.0	462.6	263.9	135.6						963.1
1957													
Inshore	13.6	11.1		156.6	159.9	73.9	.5						415.6
0–10				10.1	58.8	24.5	66.8	.3					160.5
11–20				107.0	14.9	39.8	157.7	2.5					321.9
21–45													
Offshore				117.1	73.7	64.3	224.5	2.8					482.4
1958													
Inshore			5.4	74.8	209.3	116.8	2.0			2.9			411.2
0–10			.7	203.1	1,173.0	371.3	34.1	3.9					1,786.1
11–20				.2	169.3	69.5	64.5						303.5
21–45													
Offshore			.7	203.3	1,342.3	440.8	98.6	3.9					2,089.6
1959													
Inshore													
0–10		.1		3.2	5.4	.8							9.5
11–20					1.6								1.6
21–45													
Offshore		.1		3.2	7.0	.8							11.1

See footnote at end of table.

TABLE A3.—*Pink shrimp landings*[1] *by the United States commercial fleet, Gulf of Mexico, 1956–59*—Continued

[Thousands of pounds, heads on]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
PENSACOLA—MISSISSIPPI RIVER													
1956													
Inshore			2.7	15.6	12.3	8.4	.8						39.8
0–10					5.5	42.2	11.3						59.0
11–20					112.4	271.2	294.7	2.4					680.7
21–45					2.2	2.0	9.1	7.1					20.4
Offshore					120.1	315.4	315.1	9.5					760.1
1957													
Inshore		.5	10.7	35.3	83.5	65.2	.5						195.7
0–10				.2	51.2	212.5	5.4	.2					269.5
11–20					49.2	281.7	81.5	.8					413.2
21–45					.3	3.2							3.5
Offshore				.2	100.7	497.4	86.9	1.0					686.2
1958													
Inshore	4.4		1.8	6.6	3.5	7.1	1.3	.3		13.6			38.6
0–10				3.7	2.0	26.9	20.3	.5					53.4
11–20					.5	24.5	73.9	2.7					101.6
21–45						.5	.3						.8
Offshore				3.7	2.5	51.9	94.5	3.2					155.8
1959													
Inshore			.3	10.4	30.2	9.7	3.9	.2					54.7
0–10			1.2	.5	3.0	67.2	1.8	1.7					75.4
11–20			.3	.3	10.6	30.9	71.4	24.5					138.0
21–45				.8	.3		10.4	1.5					13.0
Offshore			1.5	1.6	13.9	98.1	83.6	27.7					226.4
OBREGON—CAMPECHE													
1956													
Inshore													
0–10	212.9	205.6	261.1	136.1	171.8	164.0	80.6	32.6	9.4	31.3	7.4	242.1	1,554.9
11–20	854.7	2,034.5	1,032.0	1,321.5	1,470.3	1,538.4	2,283.2	1,561.6	1,808.0	1,709.5	1,206.7	2,774.6	19,595.0
21–45	127.2	658.3	368.5	239.6	191.4	66.1	28.1	6.4	14.0	457.4	674.6	559.6	3,391.2
Offshore	1,194.8	2,898.4	1,661.6	1,697.2	1,833.5	1,768.5	2,391.9	1,600.6	1,831.4	2,198.2	1,888.7	3,576.3	24,541.1
1957													
Inshore													
0–10	238.9	561.5	356.6	295.5	169.9	164.1	126.6	129.4	60.4	134.5	24.5	166.3	2,428.2
11–20	505.5	1,557.0	802.2	1,623.0	1,801.7	1,950.0	1,745.1	1,583.6	1,214.2	1,222.6	758.4	1,735.0	16,498.3
21–45	217.0	247.5	114.8	122.1	83.3	138.9	121.4	66.4	75.4	371.7	329.1	466.9	2,354.5
Offshore	961.4	2,366.0	1,273.6	2,040.6	2,054.9	2,253.0	1,993.1	1,779.4	1,350.0	1,728.8	1,112.0	2,368.2	21,281.0
1958													
Inshore													
0–10	108.9	347.6	280.7	210.4	204.1	119.2	91.4	42.3	45.5	41.7	32.2	129.9	1,653.9
11–20	594.0	733.8	729.9	787.9	804.9	1,178.6	1,177.6	910.1	350.4	545.7	477.3	786.4	9,076.6
21–45	187.9	319.9	191.7	208.1	49.2	35.3	40.3	29.7	2.5	59.5	590.8	984.9	2,699.8
Offshore	890.8	1,401.3	1,202.3	1,206.4	1,058.2	1,133.1	1,309.3	982.1	398.4	646.9	1,100.3	1,901.2	13,430.3
1959													
Inshore													
0–10	200.8	325.1	361.9	268.6	616.9	228.5	23.4	36.6	36.6	88.5	18.1	471.9	2,676.9
11–20	399.8	797.2	588.0	798.3	1,101.9	1,497.6	1,815.9	513.7	754.8	699.2	639.9	1,941.4	11,547.7
21–45	180.6	298.4	174.0	206.0	180.3	56.6	62.5	8.6		64.2	397.8	549.0	2,178.0
Offshore	781.2	1,420.7	1,123.9	1,272.9	1,899.1	1,782.7	1,901.8	558.9	791.4	851.9	1,055.8	2,962.3	16,402.6

[1] See table 4 (text) for summary of landings from other areas.

TABLE A4.—*White shrimp landings* [1] *by the United States commercial fleet, Gulf of Mexico, 1956–59*

[Thousands of pounds, heads on]

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
APALACHICOLA													
1956													
Inshore	0.2								168.5	143.5	156.1	2.7	471.0
0–10	9.8						7.6		.5	81.5	83.2	88.0	270.6
11–20	4.4								106.3				110.7
21–45													
Offshore	14.2						7.6		106.8	81.5	83.2	88.0	381.3
1957													
Inshore				17.0	12.9	1.5	4.2	71.6	430.8	128.0	128.0	.5	794.5
0–10	45.0	24.5	25.5	.3	43.0	5.4	1.5	.1	14.3	40.5	89.3	130.3	419.7
11–20					.1	8.6	.5		.8	23.7	32.7	1.0	67.4
21–45													
Offshore	45.0	24.5	25.5	.3	43.1	14.0	2.0	.1	15.1	64.2	122.0	131.3	487.1
1958													
Inshore			2.7	1.2	7.1	.3	.7	13.3	400.0	220.2	199.8	62.3	907.6
0–10	25.8	4.3	22.2	1.5	16.2	33.3	3.5	2.9	16.3	102.3	60.9	125.5	414.7
11–20					1.0					.8	22.8	11.1	35.7
21–45													
Offshore	25.8	4.3	22.2	1.5	17.2	33.3	3.5	2.9	16.3	103.1	83.7	136.6	450.4
1959													
Inshore	1.0	2.0			4.7	.5	.3	4.4	67.4	149.2	54.9	2.2	286.6
0–10	49.7	4.5	.5	<.1	21.9	5.9	2.5		30.6	63.3	69.9	46.2	295.0
11–20	1.3												1.3
21–45													
Offshore	51.0	4.5	.5	<.1	21.9	5.9	2.5		30.6	63.3	69.9	46.2	296.3
PENSACOLA-MISSISSIPPI RIVER													
1956													
Inshore	22.8	1.3		5.0	33.3	25.7	7.6	1,166.9	1,194.1	1,487.5	1,217.8	123.5	5,285.5
0–10	11.3	4.5	.2		3.7	10.4	4.2	47.9	88.5	281.1	425.0	128.5	1,005.3
11–20	32.1	7.7		6.4	4.9	9.1	2.0	11.1	12.8	75.3	194.7	112.1	468.2
21–45	56.8	22.2	13.6	12.8	2.5	1.5			2.5	3.4	44.2	66.0	225.5
Offshore	100.2	34.4	13.8	19.2	11.1	21.0	6.2	59.0	103.8	359.8	663.9	306.6	1,699.0
1957													
Inshore	11.1	2.7	1.3	3.2	7.2	7.1	21.8	680.9	663.3	333.1	373.9	371.6	2,477.2
0–10	14.3	1.7			7.2	8.7	5.0	27.6	31.2	38.6	42.5	6.7	183.5
11–20	42.7	5.7	1.0		6.2	4.5	1.2	24.4	42.3	59.8	95.6	67.2	350.6
21–45	22.7	1.8	.1	.2	9.7			25.7	31.7	25.5	34.6	18.6	170.6
Offshore	79.7	9.2	1.1	.2	23.1	13.2	6.2	77.7	105.2	123.9	172.7	92.5	704.7
1958													
Inshore	8.7	2.9	2.7	15.4	11.1	15.5	1.7	544.7	695.9	1,548.3	745.1	162.5	3,754.5
0–10		.5		.3	1.2	10.1	.3	8.2	20.3	110.5	172.2	57.1	380.7
11–20	5.0	17.5	.5	.5	1.0	8.4	3.2	11.4	31.2	105.0	164.6	157.8	506.1
21–45	11.9	.5	1.5		.3	6.9		5.0	22.8	64.5	164.8	48.4	326.6
Offshore	16.9	18.5	2.0	.8	2.5	25.4	3.5	24.6	74.3	280.0	501.6	263.3	1,213.4
1959													
Inshore	16.5				1.0	3.9		1,323.2	2,214.4	1,394.2	766.8	55.8	5,775.8
0–10	30.6	.7		.1	5.7	9.9	.2	28.4	159.4	324.6	299.4	81.2	940.2
11–20	75.4	1.3			.7	16.0	5.0	29.1	19.0	80.6	274.0	99.2	600.3
21–45	25.0	1.8	.8	.5	.2		2.5	.1	7.7	42.2	82.2	34.1	197.1
Offshore	131.0	3.8	.8	.6	6.6	25.9	7.7	57.6	186.1	447.4	655.6	214.5	1,737.6

See footnote at end of table.

TABLE A4.—*White shrimp landings* [1] *by the United States commercial fleet, Gulf of Mexico, 1956–59*—Continued

Area and depth (fm.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
LOUISIANA COAST													
1956													
Inshore	67.2		2.5	9.4	66.4	146.3	19.0	1,651.8	1,893.9	4,390.7	2,492.8	699.7	11,439.7
0–10	643.3	231.5	267.0	264.3	1,023.0	672.7	277.0	577.4	1,473.7	3,378.8	2,819.7	2,142.5	13,770.9
11–20	68.7	85.2	151.5	133.2	161.1	212.2	95.4	286.0	124.3	529.9	490.6	212.2	2,550.3
21–45	93.9	36.1	54.8	259.2	446.5	8.7	36.0	1.5	4.0	2.9	6.0	31.2	980.8
Offshore	805.9	352.8	473.3	656.7	1,630.6	893.6	408.4	864.9	1,602.0	3,911.6	3,316.3	2,385.9	17,302.0
1957													
Inshore	5.0		.3	10.8	4.5	5.4		696.2	651.7	1,010.0	274.7	190.3	2,848.9
0–10	685.4	451.1	304.4	270.8	358.8	371.8	.2	160.4	440.3	1,676.1	1,146.9	869.4	6,735.6
11–20	177.7	129.2	33.8	102.0	217.4	44.7	2.0	11.1	15.1	14.1	3.9	87.4	838.4
21–45	18.8	28.4	13.9	6.9	4.9			4.4		1.0	2.9	22.3	103.5
Offshore	881.9	608.7	352.1	379.7	581.1	416.5	2.2	175.9	455.4	1,691.2	1,153.7	979.1	7,677.5
1958													
Inshore	61.7		8.6		28.2	4.7		1,075.7	1,223.5	3,059.1	1,713.9	302.4	7,477.8
0–10	229.0	103.1	160.1	226.8	402.4	696.2	195.2	962.5	2,549.7	3,829.7	3,007.0	3,050.4	15,412.1
11–20	137.4	56.6	43.7	13.1	41.0	45.9	25.9	11.3	8.9	14.4	29.9	54.1	482.2
21–45	132.0	3.9	17.3	10.2	7.4	1.3	2.3	.5	2.7	237.6	65.0	119.1	599.3
Offshore	498.4	163.6	221.1	250.1	450.8	743.4	223.4	974.3	2,561.3	4,081.7	3,101.9	3,223.6	16,493.6
1959													
Inshore					20.8	16.6		1,661.4	1,831.9	2,055.6	484.5	56.4	6,127.2
0–10	423.7	50.1	59.6	266.6	507.0	386.1	113.4	1,398.4	2,182.2	5,076.3	3,761.9	1,524.9	15,750.2
11–20	132.7	18.3	1.7	23.9	137.8	111.4	21.5	57.8	347.6	139.6	134.9	203.8	1,331.0
21–45	281.7	34.1	10.4	14.1	19.0	2.0	.5	22.2	26.5	87.2	42.2	318.1	858.0
Offshore	838.1	102.5	71.7	304.6	663.8	499.5	135.4	1,478.4	2,556.3	5,303.1	3,939.0	2,046.8	17,939.2
TEXAS COAST													
1956													
Inshore			3.2	24.2	22.2	.7	5.4		686.8	420.8	155.9		1,319.2
0–10	.2	6.7	79.8	81.3	793.3	103.5	98.8	4.0	509.0	448.7	294.7	70.4	2,490.4
11–20	1.7	3.5	8.7	99.5	298.4	45.5	49.7	15.6	3.9	9.2	3.2	1.5	540.4
21–45	4.9		10.6	13.8	27.6	2.7		.8					60.4
Offshore	6.8	10.2	99.1	194.6	1,119.3	151.7	148.5	20.4	512.9	457.9	297.9	71.9	3,091.2
1957													
Inshore				10.8	9.7			209.8	1,474.4	872.8	33.6		2,611.1
0–10			2.4	10.2	36.6	30.9	2.7		256.9	243.6	269.3	54.3	906.9
11–20			1.8		2.5	5.9	1.0	.8	3.9	15.8	2.0	16.0	49.7
21–45												1.2	1.2
Offshore			4.2	10.2	39.1	36.8	3.7	.8	260.8	259.4	271.3	71.5	957.8
1958													
Inshore				2.2	75.4	37.8	43.5	335.7	1,946.4	773.1	389.6	62.8	3,666.5
0–10			34.3	240.6	109.4	164.3	15.6	460.3	1,872.0	2,506.1	894.8	810.9	7,108.3
11–20	2.0	.7	.2	5.7	45.2	27.6	.5	17.6	482.0	53.4	35.1	26.7	696.7
21–45	.5		.5	.3		.3				.2		1.7	3.5
Offshore	2.5	.7	35.0	246.6	154.6	192.2	16.1	477.9	2,354.0	2,559.7	929.9	839.3	7,808.5
1959													
Inshore				4.0	21.7		20.2	902.5	1,228.2	1,103.4	283.9	24.2	3,588.1
0–10	62.7	3.7	16.0	74.3	157.6	14.8	36.3	159.3	933.6	1,558.2	1,110.0	108.0	4,234.5
11–20	4.9		.5	3.7	74.4	11.3	20.0	47.4	55.8	80.1	60.8	74.4	433.3
21–45					1.2					0.5	.7	.8	3.2
Offshore	67.6	3.7	16.5	78.0	233.2	26.1	56.3	206.7	989.4	1,638.8	1,171.5	183.2	4,671.0

[1] See table 4 (text) for summary of landings from other areas.

TABLE A5.—*Commercial shrimp landings [1] from inshore waters along the United States Gulf coast, 1956–59*

[Thousands of pounds, heads on]

Area	1956					1957					1958					1959				
	Total	Percent species comp.				Total	Percent species comp.				Total	Percent species comp.				Total	Percent species comp.			
		B	P	W	S		B	P	W	S		B	P	W	S		B	P	W	S
Florida:																				
Charlotte Harbor																				
Tampa Bay																				
Apalachicola Bay [2]	579.8	12	10	77	1	973.2	11	12	74	3	1,236.0	25	12	63	T	297.7	16		84	
St. George Sound [2]																91.9	96		4	
St. Andrew Bay	76.1	18	64	18		94.4	51	44	5	T	61.2	6	11	83		44.2	82		18	
St. Joseph Bay																26.5	93		7	
Choctawhatchee Bay	59.5	34	61	5		49.7	35	65			69.7	60	40	T		20.2	93		7	
Pensacola Bay	326.6	25	71	4		555.4	48	40	13		674.2	55	33	12		351.3	94		6	T
Alabama:																				
Mobile Bay	1,796.8	61	T	39		1,708.4	81	3	16		1,811.0	69	T	31		1,728.8	75		25	
Perdido Bay	34.4		100								5.4	100								
Mississippi:																				
Mississippi Sound	2,990.6	53	T	47	T	3,194.2	74	4	22		2,504.4	58	1	41		5,166.0	78	1	21	
Louisiana:																				
Lake Borgne	14.3	100				340.9	30		70		1,404.0	17		83		478.3	40		60	
Lake Pontchartrain																221.8			100	
Breton Sound [2]	5,068.9	37		63	T	2,176.3	42	T	58		1,555.0	35	T	65		3,566.0	26		74	T
Chandeleur Sound [2]																1,168.6	23	T	77	
Garden Island Bay [2]											131.5	77		23	T	10.2			100	
East Bay [2]																60.6	100		T	
Bay Adam																22.7	100			
Timbalier Bay	4,790.9	46		54	T	3,815.8	77		23		2,375.7	39		59	2	4,127.4	82		18	
Barataria and Caminada Bays	8,337.2	43		57	T	4,090.3	86		14		4,298.6	46	T	53	1	6,140.6	75		25	T
Lake Salvador																132.9	100			
Little Lake																63.0			100	
Terrebonne Bay	1,902.1	40		59	1	2,562.3	84		15	1	276.7	23		77		907.9	72		28	
Caillou Bay	3,950.4	33		67	T	2,887.2	61		32	7	161.8	70		30		764.9	36		64	
Lake Barre [2]											1,428.5	T		99	1	1,221.0	58		42	
Lake Felicity [2]																435.0	100			
Lake Pelto											2,088.2	32		66	2	2,291.7	46		54	
Lake de Cade																2.9	100			
Lake Mechant											10.8			100		42.8	100			
Lost Lake											1.8	100				2.9			100	
Fourleague Bay											1,436.6	53		43	4	169.3	68		32	
Vermilion and Cote Blanche Bays	279.9			96	4	7.7			33	67	74.9	43		57		578.1			98	2
Calcasieu Lake	40.3			100		86.5			96	4	105.0			100		138.3			100	
Sabine Lake	15.0			100		1.0			100											
Texas:																				
East Bay						T			100		.7			100						
West Bay											3.2			100		13.1			100	
Galveston Bay	180.9	4		96		623.4	T		100		770.6			100		1,082.4	2		98	
Trinity Bay						120.5			100		7.7			100						
East Matagorda Bay [2]																				
Matagorda Bay [2]	609.3			100		1,492.3	14		86		1,670.3	12		88		1,457.4	6		94	
Lavaca Bay [2]																23.5			100	
San Antonio Bay [2]																339.0	22		78	
Espiritu Santo Bay [2]	285.8	2		98		335.0	47		53		333.1			100						
Mesquite Bay [2]																				
Aransas Bay [2]	304.4	41		59		1,296.3	82		18		789.3	7	T	93		573.2	1		99	
Copano Bay [2]																0.7			100	
Corpus Christi Bay [2]																294.8	1		99	
Upper Laguna Madre [2]																6.7	100			
Lower Laguna Madre [2]	264.1	74		26		273.2	40		60		668.0	40	9	51	T					
Nueces Bay [2]																3.4			100	
Baffin Bay [2]																6.6			100	

[1] Includes only shrimp taken commercially for human consumption.
[2] Data prior to 1959 are combined catches from these waters.

B—brown shrimp; P—pink shrimp; W—white shrimp; S—seabobs; T—trace, less than 1 percent.

TABLE A6.—*Comparative shrimp landings from waters off the Mexican coast of the Gulf of Mexico, 1956–57*

[Thousands of pounds, heads on]

Coastal area and subareas	Species	United States fleet		Mexican [1] fleet		Total	
		1956	1957	1956	1957	1956	1957
East Mexican Coast:							
22–30	Brown	16,374.0	23,760.2	1,503.0	1,655.2	17,877.0	25,415.4
	Pink	4.7	0	0	0	4.7	0
	White	48.3	2.5	501.1	551.5	549.4	554.0
	Total	16,427.0	23,762.7	2,004.1	2,206.7	18,431.1	25,969.4
Obregon-Campeche:							
31–35	Brown	751.1	398.2	8,617.6	8,963.5	9,368.7	9,361.7
	Pink	24,541.1	21,281.0	11,686.5	13,216.1	26,227.6	34,497.1
	White	19.6	86.4	8,779.0	9,187.2	8,798.6	9,273.6
	Total	25,311.8	21,765.6	29,083.1	31,366.8	54,394.9	53,132.4
Mexican Gulf Coast:							
22–35	Brown	17,125.1	24,158.4	10,120.6	10,618.7	27,245.7	34,777.1
	Pink	24,545.8	21,281.0	11,686.5	13,216.1	36,232.3	34,497.1
	White	67.9	88.9	9,280.1	9,738.7	9,348.0	9,827.6
	Total	41,738.8	45,528.3	31,087.2	33,573.5	72,826.0	79,101.8

[1] Data supplied by Mexican Bureau of Fisheries and Allied Industries; species composition of Mexican production based upon crude estimates.

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DEVELOPMENT AND DISTRIBUTION OF LARVAL AND JUVENILE FISHES OF THE FAMILY MULLIDAE OF THE WESTERN NORTH ATLANTIC

By MELBA C. CALDWELL, Fishery Research Biologist

BUREAU OF COMMERCIAL FISHERIES

From February 10, 1953, to December 12, 1954, the U.S. Fish and Wildlife Service made nine exploratory cruises with the motor vessel *Theodore N. Gill* into the waters off the south Atlantic coast of the United States. These cruises were the initial phase of a study of biological, chemical, and physical oceanographic conditions between Cape Hatteras and the Florida Straits. Several small specimens of goatfishes, family Mullidae, were collected. As existing keys to the group proved inadequate for the identification of the young, developmental studies were undertaken for the two species abundant in the area: *Mullus auratus* Jordan and Gilbert and *Pseudupeneus maculatus* (Bloch). Two additional species, *Upeneus parvus* Poey and *Mulloidichthys martinicus* (Cuvier), were included in the study since it was anticipated that they occurred in the waters encompassed by the survey.

Material from other than *Gill* collections has been examined. The cruises of the U.S. Fish and Wildlife Service vessels *Silver Bay* and *Oregon* have contributed many Mullidae to the collections of the Bureau of Commercial Fisheries Biological Laboratory, Brunswick, Ga. (BLBG).

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METHODS

Ernest A. Lachner is presently engaged in a revision of the family Mullidae, and I have given only as much attention to the adults as is necessary to trace development. Briggs (1958) has been followed in nomenclature.

Lachner (1951) has been followed in regard to counts of fin rays, gill rakers, and scales. All gill raker rudiments were counted as gill rakers. Photomicrographic methods of Caldwell and Carlin [1] were used for photographing specimens below 19 mm. Staining methods of Hollister (1934) and Evans (1948) were followed. Pectoral rays were counted on the right side unless the right pectoral was injured, curled, or bent forward. Measurements were made with either a micrometer eyepiece or dial calipers, and were taken at the positions indicated in figure 1.

Measurements of selected body parts less than 100 mm. are recorded to the nearest 0.1 mm., and above this size, to the nearest 0.5 mm. Measure-

[1] Caldwell, David K., and Charles R. Carlin. A photomicrographic adapter for steromicroscopes useful in photographing fish larvae. Copeia, No. 2, 1962, p. 445–446.

TABLE 1.—*Comparison of selected characters of the four species of Mullidae of the western North Atlantic*

[Applicable only to specimens of *Pseudupeneus maculatus*, *Mullus auratus*, and *Upeneus parvus* over 50 mm., and to *Mulloidichthys martinicus* over 82.5 mm. Specimen size at which development of each character occurs is discussed in the text]

Character	Species			
	P. maculatus	*M. auratus*	*U. parvus*	*M. martinicus*
Spinous dorsal fin	8 (first spine minute)	8 (first spine minute)	7	8 (first spine usually embedded in tissue and not visible).
Soft dorsal fin	I, 8	I, 8	I, 8	I, 8.
Anal fin	I, I, 6	I, I, 6	I, I, 6	I, I, 6.
Pectoral fin	13–16	15–17	14–16	15–17.
Pelvic fin	I, 5	I, 5	I, 5	I, 5.
Caudal fin	I, 7+6, I	I, 7+6, I	I, 7+6, I	I, 7+6, I.
Gill rakers:				
Total	26–32	18–21	24–27	26–33.
Lower limb	19–24	12–15	17–19	19–23.
Ceratobranchial bone	12–15	9–11	11–12	12–16 (usually 14–16).
Teeth:				
Upper jaw	Single row of canines below 100 mm.; additional large canines anterolateral to them in larger specimens.	Absent or not visible	Irregular rows of small canines.	Single row of small canines becoming irregularly biserial anteriorly.
Lower jaw	Irregular row of small canines	Single row of small canines becoming irregularly biserial anteriorly.	Irregular rows of small canines.	Single row of small canines becoming irregularly biserial anteriorly.
Vomer	Absent	Peglike teeth on fused palatovomerine bone.	Peglike	Absent.
Palatine	Absent		Peglike teeth at 54 mm. and larger.	Absent.
Lateral line scales	27–31	29–35	36–38	34–39.
Opercular spine	Present	Absent	Absent	Present.
Upper wing of cleithrum	Serrated	Smooth	Smooth	Smooth.
Branchiostegals	3	3	3	3.
Color pattern of metamorphosed specimens after preservation.	Usually retain three black blotches on side.	Pale yellow	Three or four black bars on ventral lobe of caudal fin.	Pale yellow

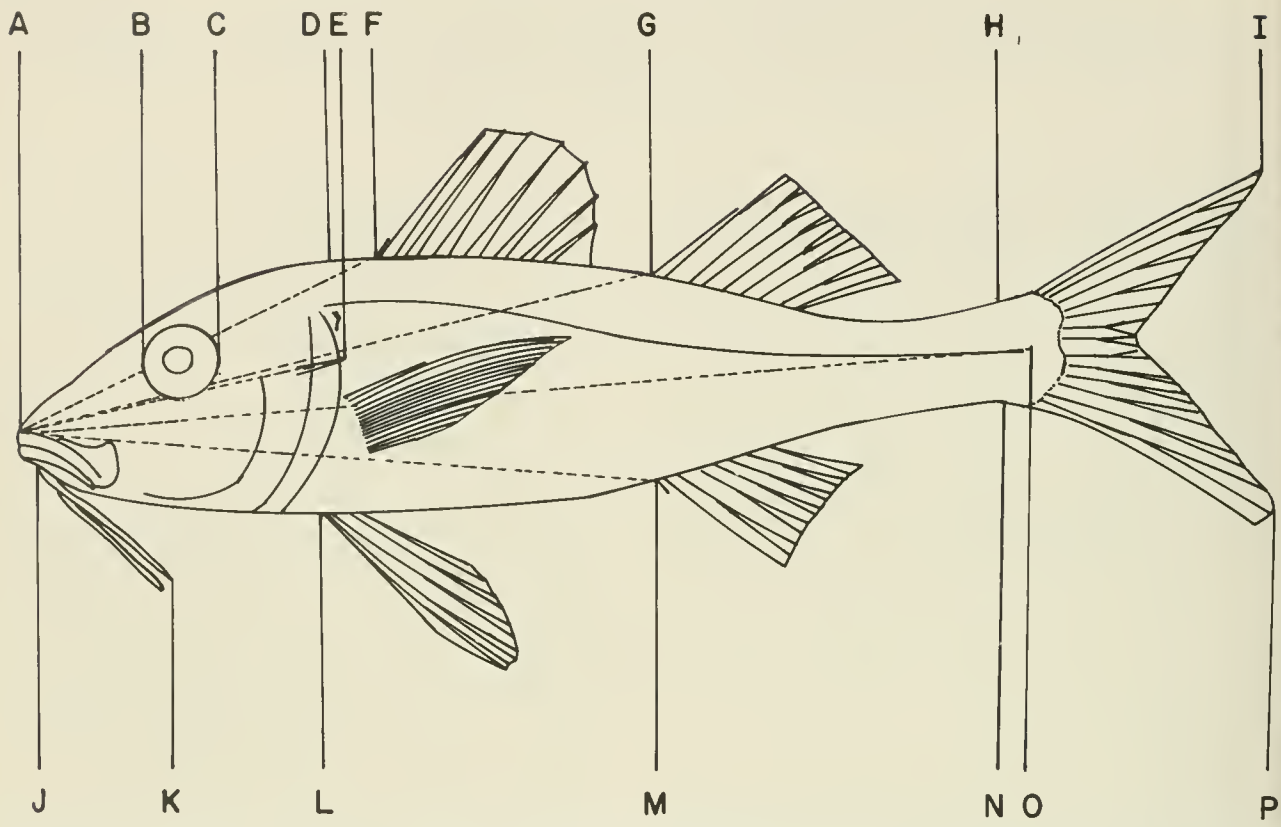

Figure 1.—*Pseudupeneus maculatus*, 48-mm. (UF uncatalogued; Dickinson collection, Bahamas.) Letters indicate points of measurements.

ments of standard length to show size range of specimens captured are indicated to the nearest 0.5 mm. All body lengths are expressed in standard length.

Percentages are indicated to the nearest 0.1 percent.

The upper lip was not included in the measurements involving the tip of snout.

A–B.—*Snout length.* Tip of snout to anterior edge of bony eye socket.

B–C.—*Eye diameter.* Horizontal width of bony eye socket.

C–E.—*Postorbital head length.* Posterior edge of bony eye socket to posterior edge of operculum, inclusive of spine if present.

A–E.—*Head length.* Tip of snout to posterior edge of operculum, inclusive of spine if present.

A–F.—*Snout to first dorsal.* Tip of snout to base of first spine of spinous dorsal.

A–G.—*Snout to second dorsal.* Tip of snout to base of first ray of soft dorsal.

A–M.—*Snout to anal.* Tip of snout to base of first spine of anal fin.

D–L.—*Depth.* Measured at deepest point, slightly anterior to first dorsal fin to origin of pelvics.

H–I.—*Dorsal lobe of caudal.* Origin of first secondary ray of dorsal lobe to tip of longest ray of dorsal lobe.

N–P.—*Ventral lobe of caudal.* Origin of first secondary ray of ventral lobe to tip of longest ray of ventral lobe.

J–K.—*Barbel length.* Anterior edge of base of barbel to tip of longest barbel.

A–O.—*Standard length.* Tip of snout to distal end of hypural bone (base of midcaudal rays).

Interorbital space. Narrowest distance between the bony eye sockets, measured on the dorsal surface.

Gill raker length. Length of first lower-limb gill raker beyond the gill raker at the angle of the arch.

Measurements were made and plotted on distance from first to second dorsal fins and caudal concavity, but the graphs are not included because of the high degree of variability and number of factors that influence these dimensions.

ABBREVIATIONS AND TERMINOLOGY

I have followed Berry (1959) in terminology of the developmental stages.

Larval.—Defined by Berry as, "the stage of development commencing with hatching and ending with the completion of formation of the adult complement of fin rays."

Only the larvae of *Mullus auratus* are considered here. In *M. auratus* the secondary rays of the caudal fin are the last rays to ossify (shown on stained material). This ossification occurs at 10 or 11 mm.

Juvenile.—Berry (1959) defined this stage as, "commencing with the end of the larval stage and terminating with the attainment of sexual maturity." All of my specimens of *P. maculatus* (smallest, 18.5 mm.), *U. parvus* (smallest, 20.8 mm.), and *Mulloidichthys martinicus* (smallest, 82.5 mm.) have reached the juvenile stage.

Adult.—Defined by Berry (1959) as, "commencing with the attainment of sexual maturity." I did not determine at what size this occurs on any of the species under consideration.

I have made no attempt to identify the chromatophores either histologically (Gordon, 1959) or chemically. I suspect, however, that in the goatfishes some of the chromatophores, particularly those in the fins, remain migratory in much larger specimens than has been shown in some other fishes (Parker, 1948).

In discussions of development of the rays, the terms "branching" and "segmentation" refer only to primary branching and segmentation in a ray. "Branching is complete" or "segmentation is complete" refer only to the fact that all rays that are to become branched or segmented have done so at least once.

Some of the specimens examined were collected in locations that are not widely known. For these I have supplied approximate latitudes and longitudes.

A few of the small specimens had no data regarding method of capture and were taken at stations listed in the vessel station lists as "longline," "hook and line," or "drift" stations. Since it is customary for participants of a cruise to use a dip net at stations and since it is improbable that a specimen under 40 mm. should have been caught by these other means, I have designated them as (D?) specimens. The abbreviations used in referring to the different collections are given on page 455. The *Gill* cruises made three different types of stations that I will refer to: Regular (Reg.), Special (Spc.), and Standard (Std.) (Anderson, Gehringer, and Cohen, 1956).

The methods of capture are indicated as follows: trawl (T), dip net (D), stomach contents (SC), market procured (M), and rotenone (R).

KEY TO MULLIDAE OF THE WESTERN NORTH ATLANTIC

Material 10.0–82.5 mm.[2]

A. Minute spine at origin of spinous dorsal (total of 8 spines) (fig. 28).
  B. Lower-limb gill rakers 11–16; over 17 mm., palato-vomerine tooth patch (fig. 31); no opercular spine (fig. 33) ..... *Mullus auratus.*
  BB. Lower-limb gill rakers 17–24; no palato-vomerine tooth patch; over 22 mm., opercular spine (fig. 23) ..... *Pseudupeneus maculatus.*

AA. No minute spine at origin of spinous dorsal (total of 7 spines) (fig. 37).
  Lower-limb gill rakers, 16–19; ceratobranchial bone gill rakers, 10–12; no opercular spine (fig. 38) ..... *Upeneus parvus.*

As no *Mulloidichthys martinicus* below 82.5 mm. have been examined or described, they are omitted from this key. Between 20 and 80 mm., they could be expected to be devoid of a visible minute spine at the origin of the spinous dorsal (fig. 40) and to have a lower-limb gill raker count of 19–23 and ceratobranchial bone gill raker count of 13–16 (allowing for formation of one additional raker between 20 and 80 mm.). As the opercular spine of *P. maculatus* is developed at 22 mm., the same trend might be expected in *M. martinicus*, a closely related species.

[2] Based upon 30 specimens of *M. auratus*, 48 *P. maculatus*, and 40 *U. parvus*.

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Material over 82 mm.[3]

A. Opercular spine (figs. 23 and 43).
  B. Scales 27–31, usually three large black blotches along lateral line (fig. 3), posterior wing of cleithrum serrated (fig. 23)_____ *Pseudupeneus maculatus.*
  BB. Scales 34–39, no black blotches along lateral line, posterior wing of cleithrum not serrated (fig. 43)_____ *Mulloidichthys martinicus.*
AA. No opercular spine.
  C. Minute first dorsal spine (fig. 28), fused palato-vomerine tooth patch (fig. 31), lower-limb gill rakers 12–15_____ *Mullus auratus.*
  CC. No minute first dorsal spine (fig. 37), separate vomer and palatine tooth patches, lower-limb gill rakers 17–19_____ *Upeneus parvus.*

COMPARISON OF SPECIES

Fishes of the family Mullidae, referred to as goatfishes or surmullets, are characterized by the presence of two barbels beneath the chin. Barbel development is discussed in the section on barbels under *M. auratus*. Larvae of juveniles which have not developed barbels, or in which the barbels have not detached from the branchiostegal membrane, can be distinguished by the presence of six to eight spines in the first dorsal fin (Jordan and Evermann, 1896) and a reduced number of branchiostegal rays (four before the barbels form, three after barbel formation). Juvenile Mullidae are most often confused with young Mugilidae, to which they bear a close superficial resemblance. Mugilidae, however, have only four spines in the first dorsal fin (Jordan and Evermann, 1896).

Table 1 (p. 403) lists the major characters of the four species of Mullidae of the western North Atlantic. The table applies only to specimens above a size of 50 mm. For specimens below 50 mm., changes which occur in the various characters are discussed for the species in their individual sections.

Fin ray counts of the spinous dorsal, soft dorsal, anal, pelvic, and caudal fins were constant throughout the size ranges examined, and ranges of pectoral ray counts are constant above 22 mm. When lateral line scales are present, counts show no variability with size of specimen. There is no change in the number of branchiostegal rays (three) after the barbels form (below 20 mm.).

Below 50 mm., the numbers of pectoral fin rays vary somewhat with size of fish.

The adult tooth patterns are not established below 50 mm., and in *P. maculatus*, not before 100 mm.

The opercular spine of *P. maculatus* (and presumbaly *M. martinicus*) is apparent at 21.9 mm. The serrated upper wing of the cleithrum in *P. maculatus*, however, is not obvious below 50 mm.

Adult color patterns become established after metamorphosis, which occurs between 40 and 70 mm.

Morphometric relationships are shown graphically in figures 9 through 21 (p. 415–427).

ECOLOGY OF THE MULLIDAE

Thorson (1957) estimated that 85 to 90 percent of all species in tropical level-bottom communities have a long pelagic life, and two-thirds (on the average) of the level-bottom animals of the boreal seas have pelagic larvae. Hubbs (1941) has pointed out that fishes inhabiting rocks, sand, or weed may have a pelagic stage which is quite different from the adult. The difference is so marked in some species that the two stages have been described and named as different species by competent ichthyologists (Hubbs, 1958; Breder, 1949). In a recent paper Caldwell (1962) has given a detailed analysis of this transformation in *Pseudopriacanthus altus* (Gill).

Four of the six genera of this family are represented in the western North Atlantic. The young of *P. maculatus*, *M. auratus*, and *U. parvus*, representing three of the four genera in the western North Atlantic, have a pelagic stage differing in body shape and coloration from a subsequent inshore stage. A pelagic stage is also indicated within the genus *Parupeneus*. Gosline and Brock (1960) commented that the young of *Parupeneus porphyreus* (Jenkins), a Pacific mullid, appear in shallow water at approximately 40 mm.

As no *M. martinicus* smaller than 82.5 mm. have been taken, the possibility exists that this species does not have a pelagic stage. In addition, I have examined approximately 50 collections of premetamorphosed mullids from the Pacific coast of

[3] Based upon 16 specimens of *P. maculatus*, 27 *M. martinicus*, 20 *M. auratus*, and 11 *U. parvus*.

the Americas and again failed to find any specimen smaller than 72 mm. of the genus *Mulloidichthys*, although at least one species of this genus is not uncommon there. However, there are several other factors that could account for a failure to collect smaller specimens; e.g., failure to collect in the proper locality, failure of this species to come to a night light, and the possibility that this is a diurnal rather than a nocturnal species.

Major physical changes occurring in these fishes following the attainment of a benthic habitat are replacement of the silvery or dark brown pelagic coloration by the adult coloration and the acquisition of a more robust body shape.

The scales of the small pelagic speciments shed easily, whereas those of even the smallest metamorphosed specimens are much more firmly fixed.

PSEUDUPENEUS MACULATUS (BLOCH)

Sources of material and pertinent station data are listed (table 2), and the locations of capture are shown (fig. 2).

DISTRIBUTION

Briggs (1958) gave the range of *Pseudupeneus maculatus* as "New Jersey and Bermuda to Rio de Janeiro and the southern and northeastern Gulf of Mexico."

One specimen (table 2) was procured slightly south of Rio de Janeiro (Santos, Brazil). This was probably a market specimen, and the exact location of its initial capture is uncertain.

On two occasions, juveniles were captured in the Gulf of Mexico in other than the southern or northeastern sectors (fig. 2). These were pelagic specimens, and the locations of capture indicate

Figure 2.—Locations of capture of *Pseudupeneus maculatus* and *Upeneus parvus*.

TABLE 2.—*Collection and station data for 274 specimens of* Pseudupeneus maculatus *examined*

[Dip net (D), trawl (T), stomach contents (SC), collected with rotenone (R), and market procured (M)]

Station	Latitude	Longitude	Date of capture	Depth of water in which captured	Method of capture	Number of specimens and size range	Collection and catalogue number (if any)
				Fathoms		*mm.*	
WESTERN NORTH ATLANTIC:							
Gill Cr. 2, Reg. 71	34°04′ N.	76°15′ W.	May 9, 1953	16	D	(1) 48.5	BLBG
Silver Bay 1218	33°45′ N.	76°50′ W.	Sept. 3, 1959	23–24	T	(10) 107.0–206.5	BLBG
Gill Cr. 4, Reg. 65	33°42′ N.	76°56′ W.	Nov. 9, 1953	22	D	(1) 18.5	BLBG
Gill Cr. 2, Reg. 63	33°15′ N.	76°23′ W.	May 8, 1953	412	D	(4) 33.0–46.0	BLBG
Gill Cr. 2, Reg. 49	32°12′ N.	78°25′ W.	May 6, 1953	185	D	(1) 43.5	BLBG
Gill Cr. 2, Reg. 42	31°57′ N.	79°18′ W.	May 6, 1953	75	D	(2) 42.0 and 44.0	BLBG
Silver Bay 1549	30°40′ N.	80°15′ W.	Jan. 17, 1960	22–25	T	(1) 160.0	BLBG
Silver Bay 1534	30°39′ N.	80°17′ W.	Jan. 15, 1960	22–23	T	(11) 147.5–198.0	BLBG
Gill Cr. 2, Reg. 20–21	29°40′ N.	80°57′ W.	Apr. 26, 1953	9–15	D	(1) 37.0	BLBG
Silver Bay 1553	29°39′ N.	81°06′ W.	Jan. 19, 1960	9–10	T	(1) 145.5	BLBG
Combat 343	29°19′ N.	80°18′ W.	June 1, 1957	[1] 30	D	(23) 35.0–41.0	BLBG
Gill Cr. 6, Reg. 10	28°20′ N.	80°10′ W.	Apr. 27, 1954	21	D	(2) 45.0 and 47.0	BLBG
Gill Cr. 2, Reg. 8	28°19′ N.	79°26′ W.	Apr. 24, 1953	435	D	(1) 49.0	BLBG
Gill Cr. 5, Spc. Sta. 9	28°00′ N.	79°00′ W.	Feb. 1, 1954	455	D	(16) 48.0–54.0	BLBG
Gill Cr. 2, Reg. 5–6	27°42′ N.	79°46′ W.	Apr. 23, 1953	27–310	SC	(2) 38.5 and 41.0 [2]	BLBG
Gill Cr. 5, Reg. 5	27°40′ N.	80°04′ W.	Jan. 30, 1954	20	D	(1) 42.0	BLBG
Gill Cr. 6, Reg. 5	27°40′ N.	80°04′ W.	Apr. 26, 1954	20	D	(1) 46.0	BLBG
Gill Cr. 1	27°20′ N.	78°00′ W.	Feb. 12, 1953		SC	(2) 40.0 and 44.0 [3]	BLBG
Gill Cr. 6, Reg. 4	27°20′ N.	80°04′ W.	Apr. 26, 1954	13	D	(3) 44.0–45.0	BLBG
Gill Cr. 2, Reg. 3	27°01′ N.	80°04′ W.	Apr. 23, 1953	6	D	(1) 39.0	BLBG
Gill Cr. 4, Reg. 1	27°00′ N.	79°18′ W.	Oct. 12, 1953	356	D	(1) 39.0	BLBG
Gill Cr. 3, Reg. 3	27°00′ N.	80°04′ W.	July 25, 1953	9	D	(1) 40.0	BLBG
Gill Cr. 1, Abaco Light, Anchorage	[4] 25°51′ N.	77°10′ W.	Feb. 15, 1953	[1] 11	D	(10) 54.5–61.0	BLBG
Cat Cay, Grand Bahama Bank	[4] 25°35′ N.	79°15′ W.	July 23, 1955		D	(2) 42.0 and 43.0	BLGT
Cat Cay, Grand Bahama Bank	[4] 25°35′ N.	79°15′ W.	July 14, 1955		D	(6) 38.0–45.0	BLGT
Gill Cr. 5, Near Eleuthera Island, Bahamas.	[4] 25°32′ N.	76°13′ W.	Jan. 27–28, 1954	[1] 1000 to 2000	D	(1) 58.0	BLBG
Gill Cr. 5, Near Eleuthera Island, Bahamas.	[4] 25°32′ N.	76°13′ W.	Jan. 27, 1954	[1] 1000 to 2000	D	(1) 59.5	BLBG
Treasure Island (Salt Cay), Bahamas.	25°06′ N.	77°17′ W.	Aug. 14, 1955	0–2	R	(2) 41.0 and 140.5	ANSP 84851
New Providence Island, Bahamas	25°06′ N.	77°20′ W.	Mar. 23, 1955	17	D	(8) 50.0–56.0	ANSP 84838
Silver Cay, Bahamas	25°06′ N.	77°22′ W.	Apr. 5, 1955	1	R	(25) 49.0–73.5	ANSP 84840
12 mi. west of Nassau, Bahamas	[4] 25°05′ N.	77°24′ W.	July 9, 1958	1	R	(3) 48.0–57.5	UF
Nassau Market, Bahamas			Aug. 17–20, 1955		M	(1) 225.0	UF 3533
Key West, Florida						(1) 69.5	CAS IUM 8509
Key West, Florida						(6) 40.0–62.5	CAS IUM 2400
Key West, Florida						(6) 45.5–81.0	SU 2399
GULF OF MEXICO:							
Garden Key, Florida	[4] 24°38′ N.	82°54′ W.				(2) 48.5 and 50.0	SU 3200
Oregon 1313	28°05′ N.	88°46′ W.	June 9, 1955	980	D	(1) 21.5	CNHM 64714
Oregon 1035	26°40′ N.	92°00′ W.	May 8, 1954	890	D	(1) 43.5	USNM 64712
Oregon 1074	24°00′ N.	96°50′ W.	May 25, 1954	575	D	(1) 47.0	BLBG
Silver Bay 403	22°12′ N.	89°57′ W.	May 11, 1958	27	D	(5) 41.5–45.0	BLBG
Silver Bay 410	21°13′ N.	89°50′ W.	May 12, 1958	27	D	(1) 42.5	BLBG
Oregon 2174	22°23′ N.	89°44′ W.	May 11–12, 1958	15	D	(11) 42.0–51.0	USFWS Ieth. Lab.
STRAITS OF FLORIDA:							
Oregon 780	23°30′ N.	82°26′ W.	May 9–10, 1953	900	D	(1) 47.5	TU 5985
CARIBBEAN SEA:							
Oregon 786	21°45′ N.	84°40′ W.	May 15, 1953		D	(4) 44.0–55.0	TU 5991
Oregon 1297	20°50′ N.	86°10′ W.	Apr. 28, 1955	800	D	(11) 41.5–49.0	BLGT
Misterioso Bank off Yucatan, Mexico.			Jan. 4, 1940			(1) 40.0	CNHM 39673
Misterioso Bank off Yucatan, Mexico.			Jan. 4, 1940			(1) 40.5	CNHM 39674
Misterioso Bank off Yucatan, Mexico.			Jan. 4, 1940			(1) 29.0	CNHM 39675
Oregon 1863	16°22′ N.	83°31′ W.	Aug. 20, 1957	165–170	D	(1) 49.0	BLBG
Havana, Cuba						(4) 45.0–159.0	SU 1826
Cuba						(1) 59.0	CAS IUM 11285
Cuba						(1) 144.0	CAS IUM 2642
Eaton Hall Cove, Jamaica	[4] 18°27′ N.	77°20′ W.	Jun. 14, 1958	1	R	(1) 53.5	DKC#C6-1458-1J
Rocky Point Market, Jamaica					M	(1) 171.0	DKC
Kingston Market, Jamaica			Apr. 24, 1959		M	(2) 147.0 and 182.0	DKC
Kingston Market, Jamaica					M	(1) 151.0	DKC
Puerto Rico						(2) 59.0–64.0	CAS IUM 9477
St. Croix, Lesser Antilles						(1) 157.0	CAS IUM 12374
Oregon 2617	18°51′ N.	64°38′ W.	Sept. 27, 1959	41	T	(6) 77.5–103.5	BLBG
Oregon 2625	18°45′ N.	64°47′ W.	Sept. 28, 1959	38	T	(1) 85.0	BLBG
Oregon 2608	18°35′ N.	65°03′ W.	Sept. 26, 1959	42	T	(10) 83.5–155.5	BLBG
Oregon 2619	18°15′ N.	64°49′ W.	Sept. 27, 1959	26	T	(3) 89.0–106.5	BLBG
Oregon 2618	18°15′ N.	64°45′ W.	Sept. 27, 1959	29	T	(17) 67.0–127.0	BLBG
Oregon 2631	17°28′ N.	63°32′ W.	Sept. 30, 1959	19	T	(7) 71.0–110.0	BLBG
British West Indies						(4) 132.5–199.5	SU 4877
WESTERN SOUTH ATLANTIC:							
Recife, Brazil	08°03′ S.	34°51′ W.				(1) 161.5	SU 52249
Bahia, (Salvadore) Brazil	13°00′ S.	38°31′ W.				(3) 79.0–120.5	SU 1735
Bahia, (Salvadore) Brazil	13°00′ S.	38°31′ W.				(1) 113.0	CAS IUM 8534
Vitoria, Brazil	20°18′ S.	40°20′ W.				(5) 58.0–103.0	SU 52247
Santos, Brazil	23°50′ S.	46°40′ W.				(1) 132.0	SU 52248

[1] Estimated from hydrographic chart.
[2] Stomach contents of *Coryphaena hippurus* Linnaeus.
[3] Stomach contents of *Thunnus orgentivittatus* (Cuv. and Val.).
[4] Approximate latitude and longitude.

that they were carried there by a branch of the Gulf Stream (Leipper, 1954).

ECOLOGY

Parr (1930) called attention to two color stages of *P. maculatus* taken in the Bahamas and Turks Island: a blue pelagic form that he took by surface light at night and a more highly colored benthonic stage obtained in a small bottom trawl and never observed at the surface. He observed, ". . . it would seem that the change from the pelagic existence of the young to the benthonic life of the adults does not occur until the fish has reached a length without caudal fin of about 70 mm. . . ."

Figure 3 shows two specimens of *P. maculatus*, 41.0 mm. and 59.5 mm., which exhibit distinctly different body shapes and pigmentation. The smaller one was taken with the aid of rotenone in 1 fathom of water, and the larger individual was dip netted over deep water. Although the specimens are superficially unlike, they both show the characters of *P. maculatus* (table 1). The smaller metamorphosed specimen is developing the three dark blotches which, among the western North Atlantic Mullidae, are peculiar to *P. maculatus*.

Figure 4 shows a series of pelagic specimens dip netted by night light.

I examined another series of 25 young *P. maculatus* from the Bahamas that were apparently undergoing metamorphosis when taken. All characters were those of *P. maculatus*, and some were developing indications of the three dark blotches peculiar to this species (fig. 5, uppermost). This series (fig. 5) was light tan in color as opposed to the dark dip-netted specimens, and for the most part, more robust in body contour (fig. 5, uppermost). Some of the smaller forms, however, had the long slender shape of the pelagic form (fig. 5, lowermost).

Figure 3.—*Upper*, Bottom-living 41.0-mm. *Pseudupeneus maculatus*. Collected with rotenone in less than 2 fathoms (ANSP 84851; Bohlke collection, Bahamas). *Lower*, Pelagic 59.5-mm. *Pseudupeneus maculatus*. Dip netted over 1,000–2,000 fathoms, by *Gill* personnel. (BLBG)

All of the specimens shown in figures 3, 4, 5, 6, and 7 are juveniles of *P. maculatus*. Figure 6 shows metamorphosed (upper) and pelagic (lower) specimens of similar size for comparison.

The small specimens up to 61.0 mm. were taken by dip net or with aid of rotenone. With one exception, the dip-netted specimens had long, slender, dark bodies typical of pelagic fish. The one exception, a 43.0-mm. specimen, had begun to acquire the three black pigmentation blotches peculiar to *P. maculatus*. The fact that this stage was dip netted over depths as great as 1,000 to 2,000 fathoms (table 2) is evidence of their pelagic mode of life.

The smallest specimen taken by bottom trawl was 67.0 mm. (table 2), and this and all trawled specimens had attained the coloration and most of the body shape of the adult. That these were routinely trawled from the bottom in depths not exceeding 42 fathoms is indication of their shallow-water, bottom-living mode of life. They have also been observed and photographed in this habitat (Longley and Hildebrand, 1941).

When the sizes of specimens, depths of capture, and methods of capture are plotted (table 3, p. 411) the different habitats of the adults and juveniles become apparent. The shallow-water specimens ranged from 41.0 mm. upward, and all of

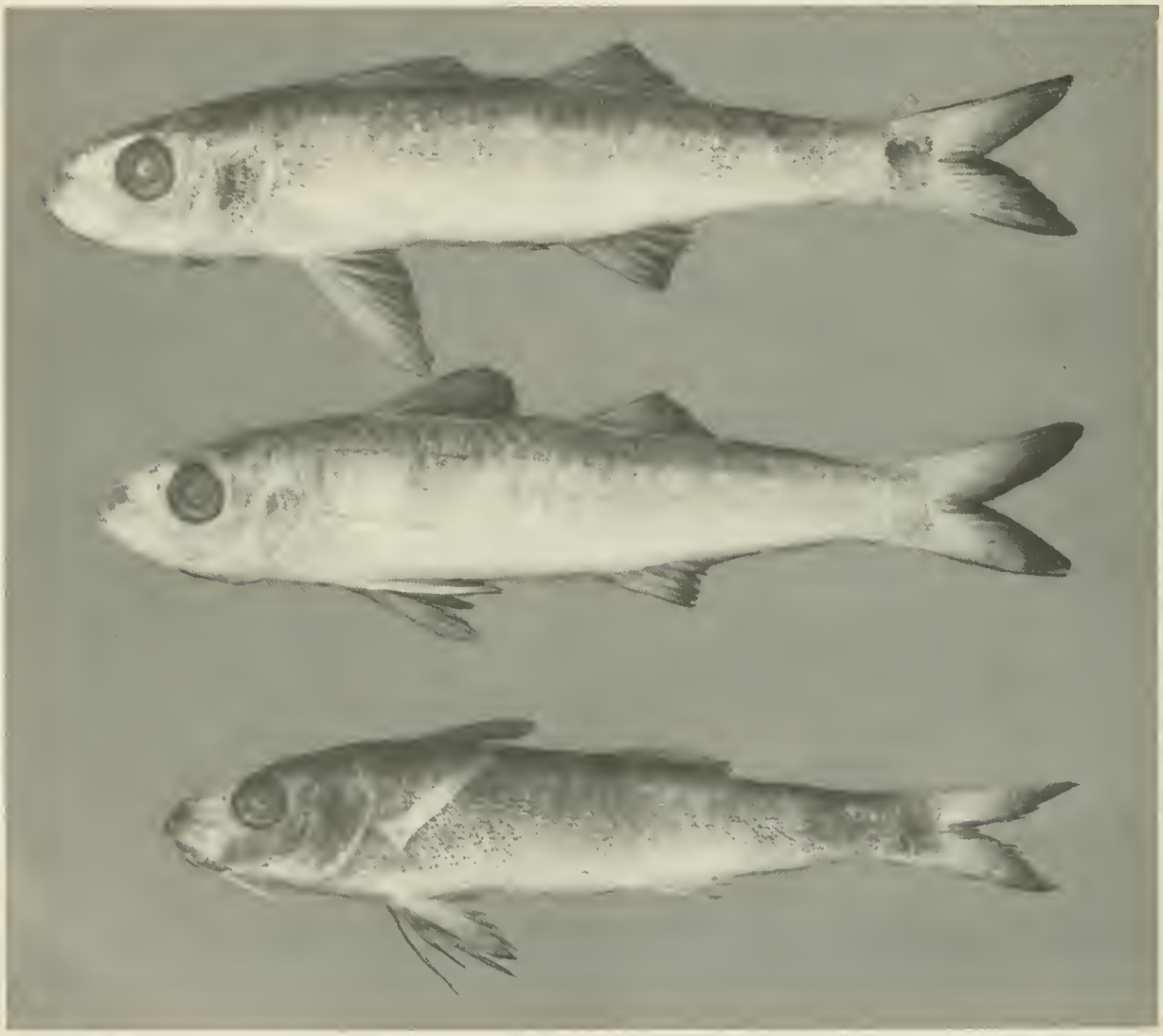

Figure 4.—Pelagic *Pseudupeneus maculatus*. From top to bottom, 53.5 mm., 50.2 mm., and 46.5 mm. Dip netted by *Gill* personnel. (BLBG)

TABLE 3.—*Relation of size of specimen, method of capture, (dip net, D; trawl, T; collected with rotenone, R), and water depths in which captured for* Pseudupeneus maculatus

[Each letter represents the capture of one or more specimens within a particular size range]

DEPTH IN FATHOMS	SIZE RANGE IN MILLIMETERS				
	0–24.5	25.0–49.5	50.0–74.5	75.0–99.5	Over 100
Over 100	D	DDDD DD	DDDD DDD		
75–99					
50–74			D		
25–49		DDD		TTTT	TTT
3–24	D	DDDD DDDD D	DD		TTTT
0–2		RRR	RRR		R

TABLE 4.—*Relation of numbers of pectoral fin rays to standard length of 58 specimens of* Pseudupeneus maculatus

[The upper number is the number of specimens, and the number in parentheses below is the approximate percentage for the respective size range]

Standard length (mm.)	Number of pectoral rays					Number of specimens
	13	14	15	16	17	
0–19.9			1 (100)			1
20.0–29.9			2 (100)			2
30.0–39.9		1 (16.7)	1 (16.7)	3 (50.0)	1 (16.7)	6
40.0–49.9		1 (12.5)	3 (37.5)	4 (50.0)		8
50.0–74.9	1 (4.5)		5 (22.7)	16 (72.7)		22
75.0–99.9			5 (83.3)	1 (16.7)		6
100.0–124.5			1 (33.3)	2 (66.6)		3
125.0–149.5			2 (66.6)	1 (33.3)		3
150.0–200.0			4 (80.0)	1 (20.0)		5

TABLE 5.—*Relation of total numbers of gill rakers to standard length of 60 specimens of* Pseudupeneus maculatus

[The upper number is the number of specimens, and the number in parentheses below is the approximate percentage for the respective size range]

Standard length (mm.)	Number of gill rakers									Number of specimens
	24	25	26	27	28	29	30	31	32	
0–29.9			1 (100)							1
30.0–39.9	1 (16.7)		1 (16.7)	2 (33.3)	2 (33.3)					6
40.0–49.9				3 (37.5)	2 (25.0)	2 (25.0)	1 (12.5)			8
50.0–74.9			1 (3.6)		5 (17.9)	9 (32.1)	6 (21.4)	4 (14.3)	3 (10.7)	28
75.0–99.9				1 (16.7)	4 (66.7)	1 (16.7)				6
100.0–124.5				2 (66.7)				1 (33.3)		3
125.0–149.5			2 (66.7)		1 (33.3)					3
150.0–200.0			1 (20.0)	3 (60.0)	1 (20.0)					5

these had light pigmentation. The body shape of most of them had begun transforming, but some had not (fig. 5, lowermost).

The largest pelagic specimen, 61.0 mm., was taken over shallow water (less than 11 fathoms), but very close to deep water and on a day when the seas were extremely rough. The wind was from the southwest and the 100-fathom line less than a mile southwest of Abaco Light, with the 1,000-fathom line being only about 4 miles distant. The next largest, 58.0 and 59.5 mm., were taken over water depths between 1,000 and 2,000 fathoms. These were juveniles which probably had not found shallow water in which to settle. There was no evidence of color transformation. The transforming 43.0-mm. specimen mentioned above, dip netted over 27 fathoms, was light colored and had begun to acquire the three characteristic lateral blotches of the species. Since it was dip netted over shallow water there is the possibility that it had settled to the bottom and returned to the surface. It showed no evidence of injury.

Thus it seems that *P. maculatus* has two juvenile stages—the first pelagic and the second a shallow-water, bottom-living stage. The pelagic stage is retained until the fish either finds shallow water,

Figure 5.—Collected with rotenone, bottom-living, transforming *Pseudupeneus maculatus*. From top to bottom, 56.5 mm., 51.5 mm., and 49.5 mm. (ANSP 84840; Böhlke collection, Bahamas.)

or, at some size over approximately 61 mm. (the largest dip netted), it may be lost.

The first indication of metamorphosis is loss of the overall dark pigmentation and formation of three black blotches along the lateral line. This is followed by an elevation of both the back and head (also see *P. maculatus*, Sexual Dimorphism). The abrupt increase in body depth is indicated on the graph (fig. 12).

In the inset in figure 12, the dip-netted specimens (long and slender, and silvery or dark brown) are indicated separately from the transforming and transformed specimens caught either by bottom trawl or with the aid of rotenone. The transforming 43.0-mm., dip-netted specimen mentioned above is omitted. Between 40 and 60 mm., the specimens that were still pelagic showed a downward inflection of the depth slope, whereas an upward inflection is demonstrated for the metamorphosing forms.

Figure 6.—*Upper.* 59.0-mm. metamorphosed *Pseudupeneus maculatus* (CAS IUM 9477). *Lower.* 58.9 mm. pelagic *Pseudupeneus maculatus.* Dip netted by *Gill* personnel. (BLBG)

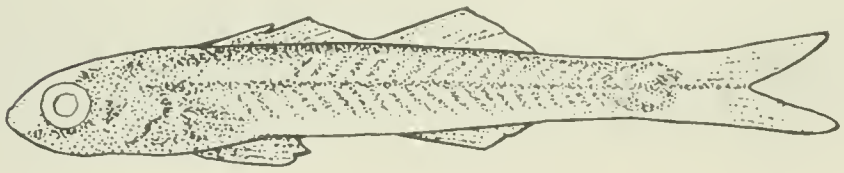

Figure 7.—*Pseudupeneus maculatus*, 18.5 mm. Dip netted by *Gill* personnel. (BLBG)

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GROWTH AND DEVELOPMENT

The smallest *P. maculatus* examined was 18.5 mm. (fig. 7). The presence of a minute first dorsal spine, absence of a palato-vomerine tooth patch, and characteristic pigmentation served to identify this species at this size. The secondary caudal rays, 9 on the dorsal lobe and 10 on the ventral lobe, have ossified and, by my definition, this specimen was a juvenile.

There are no major changes occurring until the juvenile (fig. 4) goes to the bottom and transforms (fig. 5). In the material that I examined, this usually occurred between 40 and 60 mm. At 94.7 mm. (fig. 8) the juvenile has assumed the general appearance of the adult.

Body proportions

Thirteen of the body dimensions measured on 66 specimens selected for size were chosen to depict development of various body proportions. Twenty-one of the 66 were of a series of 25 transforming specimens, ranging from 49.5 to 73.5 mm., taken with the aid of rotenone in less than 1 fathom of water (table 2). Body depth was determined for several additional 40- to 60-mm. pelagic specimens to reveal more clearly the sudden increase in this dimension in this size range. These original measurements are plotted against standard length in figures 9 through 21. The data suggest the inflection in slope for body dimensions to coincide with, or appear shortly after, the size range in which the species changes habitats.

For three of the dimensions, head length (fig. 9), postorbital head length (fig. 10), and snout to anal fin (fig. 11), the rate of increase is constant from the smallest through the largest specimens.

For body depth a straight line can be fitted to the data (fig. 12). In the 50- to 60-mm. size range, however, the pelagic forms are all below the line, and the bottom-dwelling forms are above the line (inset), suggesting sudden increase in this dimension initially upon assumption of a bottom habitat and a cessation of depth growth for pelagic forms in this range. The resumption of the initial rate of increase beyond this transformation period suggests this to be a temporary phenomenon.

Beyond 70- to 80-mm. the rate of increase of eye diameter is constant and slightly lower than the initial rate (fig. 13).

The data for the measurement, snout to spinous dorsal fin (fig. 14), suggest one rate of increase to about 50 mm. and a second slightly higher and constant rate beyond about 60 mm.; but rather than a simple inflection at 50 to 60 mm., there is an upward shift, indicating a sudden increase in this dimension in this range.

The rate of increase for snout to soft dorsal fin (fig. 15) beyond an inflection at about 50 to 60 mm. is constant and slightly higher than the initial rate.

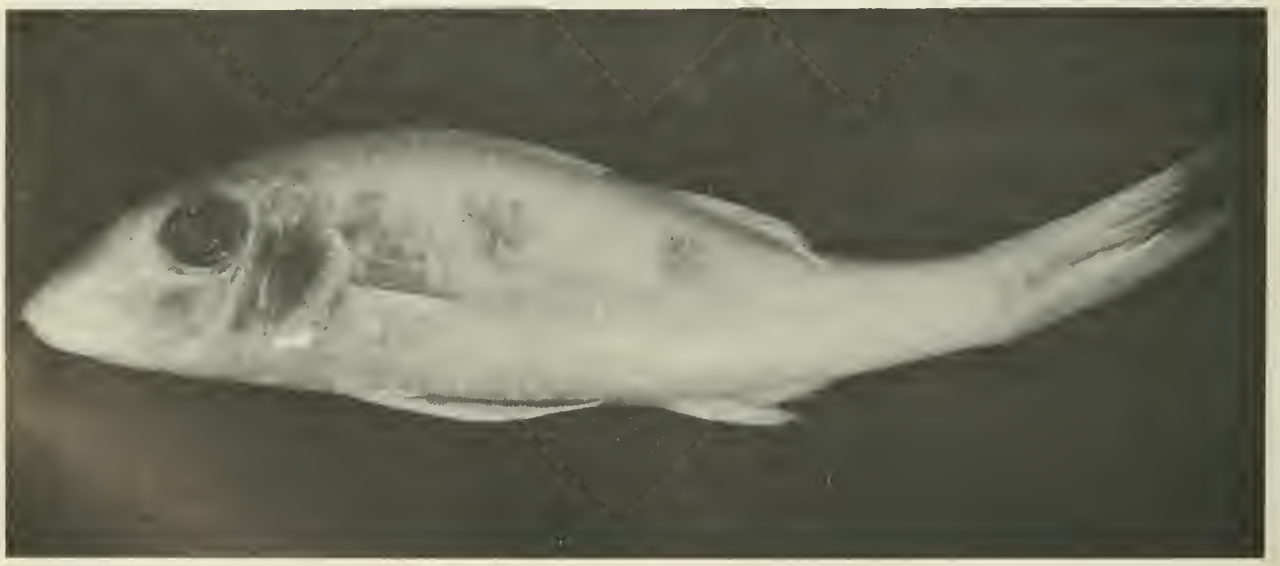

Figure 8.—*Pseudupeneus maculatus*, 94.7 mm. Trawled by *Oregon* personnel. (BLBG)

For length of ventral lobe of caudal fin (fig. 16) the rates of increase to about 60 mm. and beyond 100 mm. are constant and similar. There is an upward shift in the line depicting the ultimate rate in the 70- to 100-mm. size range. For length of dorsal lobe and caudal fin (fig. 17) there is an inflection at 80 to 100 mm. with the initial rate of increase slightly higher than the ultimate rate.

Interorbital space (fig. 18) appears to experience similar and constant rates of increase below about 40 mm. and above about 60 mm., with a considerable lower rate of increase in the 40- to 60-mm. size range. An inflection occurs in data for length of barbel (fig. 19) between 45 and 55 mm., with the rate of increase constant and lower beyond the inflection than initially.

For snout length (fig. 20) the rate of increase beyond an inflection at 40 to 50 mm. is constant and higher than the initial rate.

For length of the first lower-limb gill raker (fig. 21) there is apparently no increase between the smallest size in which raker lengths was determined (about 21.6 mm.) and about 55 mm. Beyond 55 mm. this part increases in length at a constant rate through the largest size examined.

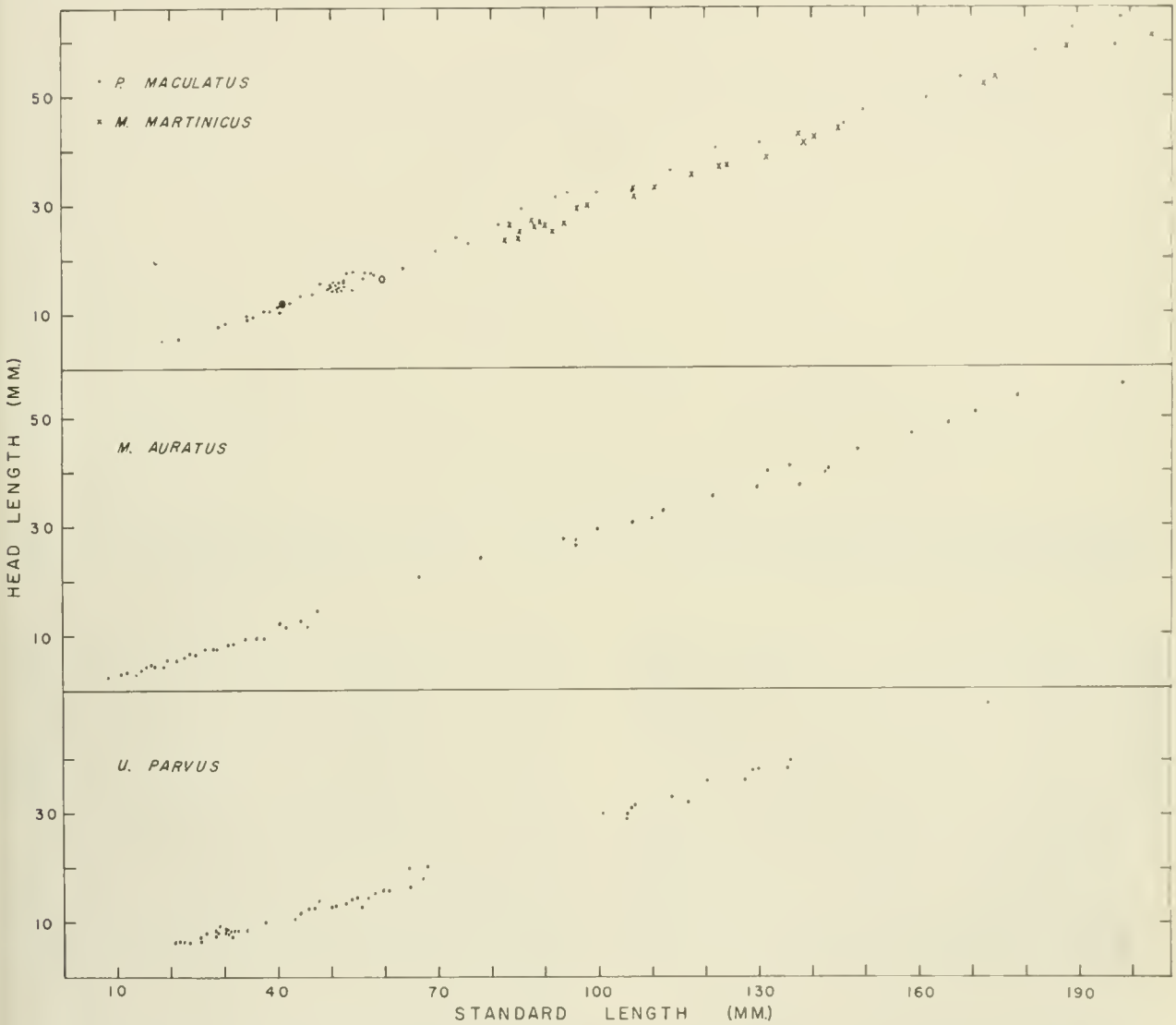

Figure 9.—Relation of head length to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

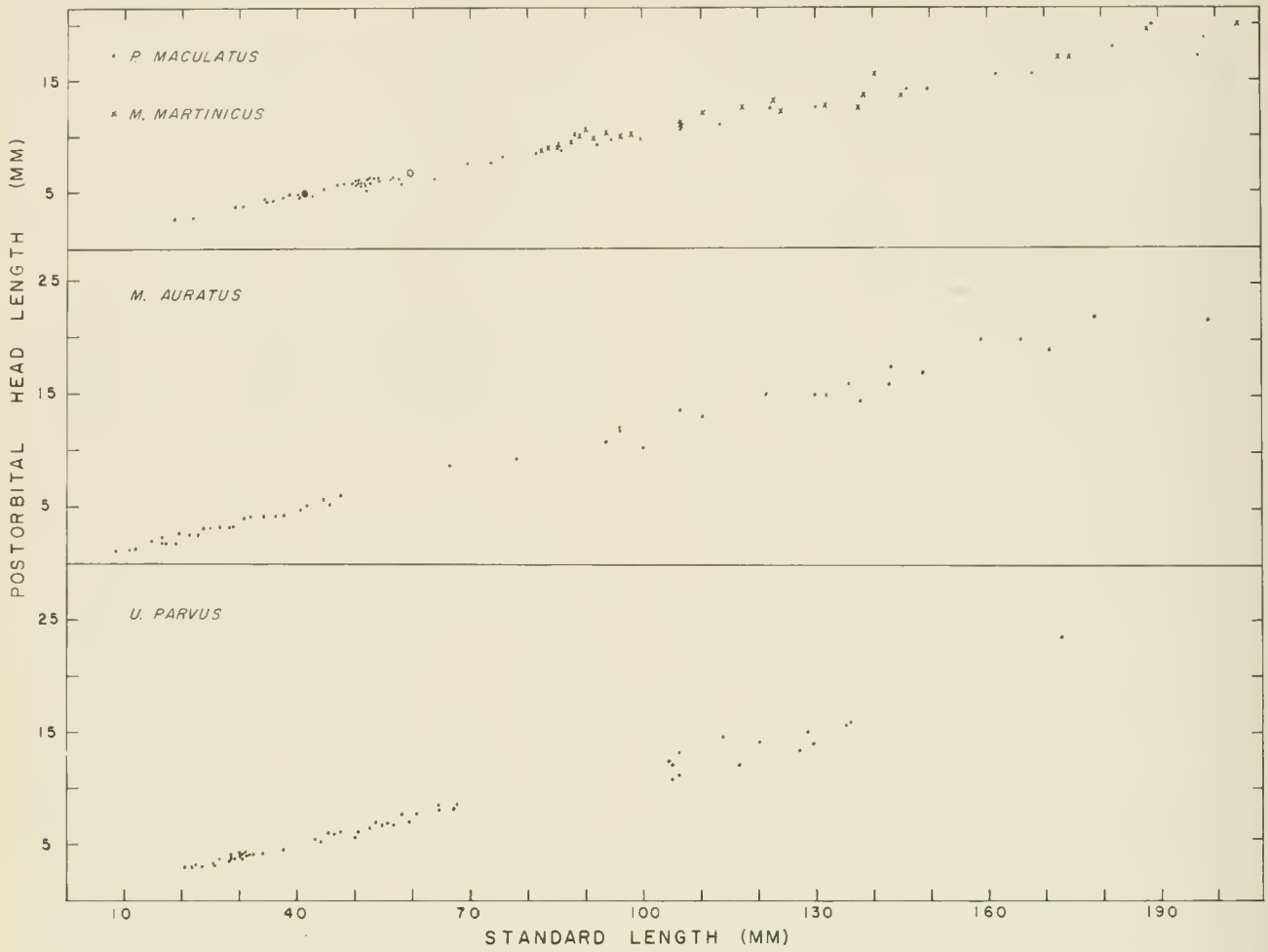

Figure 10.—Relation of postorbital head length to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

The measurements of the smallest metamorphosed specimen (41.0 mm.) captured with aid of rotenone in a water depth not exceeding 2 fathoms (fig. 3, upper), and of one of the largest pelagic specimens (59.5 mm.) dip netted over a water depth of 1,000 to 2,000 fathoms (fig. 3, lower), suggest the differences between dimensions of metamorphosing or metamorphosed specimens and those of pelagic specimens. All of the specimens below 40 mm. were dip netted and pelagic, and all of the specimens above 50 mm. were taken with aid of rotenone or were trawled, and were bottom-living, with the 59.5-mm. exception.

Pigmentation

The pelagic juveniles were preserved in formalin, and the transitional and metamorphosed forms were preserved in isopropyl alcohol after being fixed in formalin. An 18.5-mm. specimen (fig. 7) was dark tan overall. In lateral view it had a row of large chromatophores along the entire lateral midline. They were set so closely together that they gave the impression of a solid line. This impression was heightened by the closely set, needle-thin fingers of dark brown pigmentation spreading from the matrices of these chromatophores. Above the lateral midline the fingers spread obliquely upward and posteriorly; below the lateral midline the fingers pointed obliquely forward and ventrally. Immediately below the dorsal fins there was a second row of pigment spots paralleling the row along the lateral midline. Above and below the lateral midline,

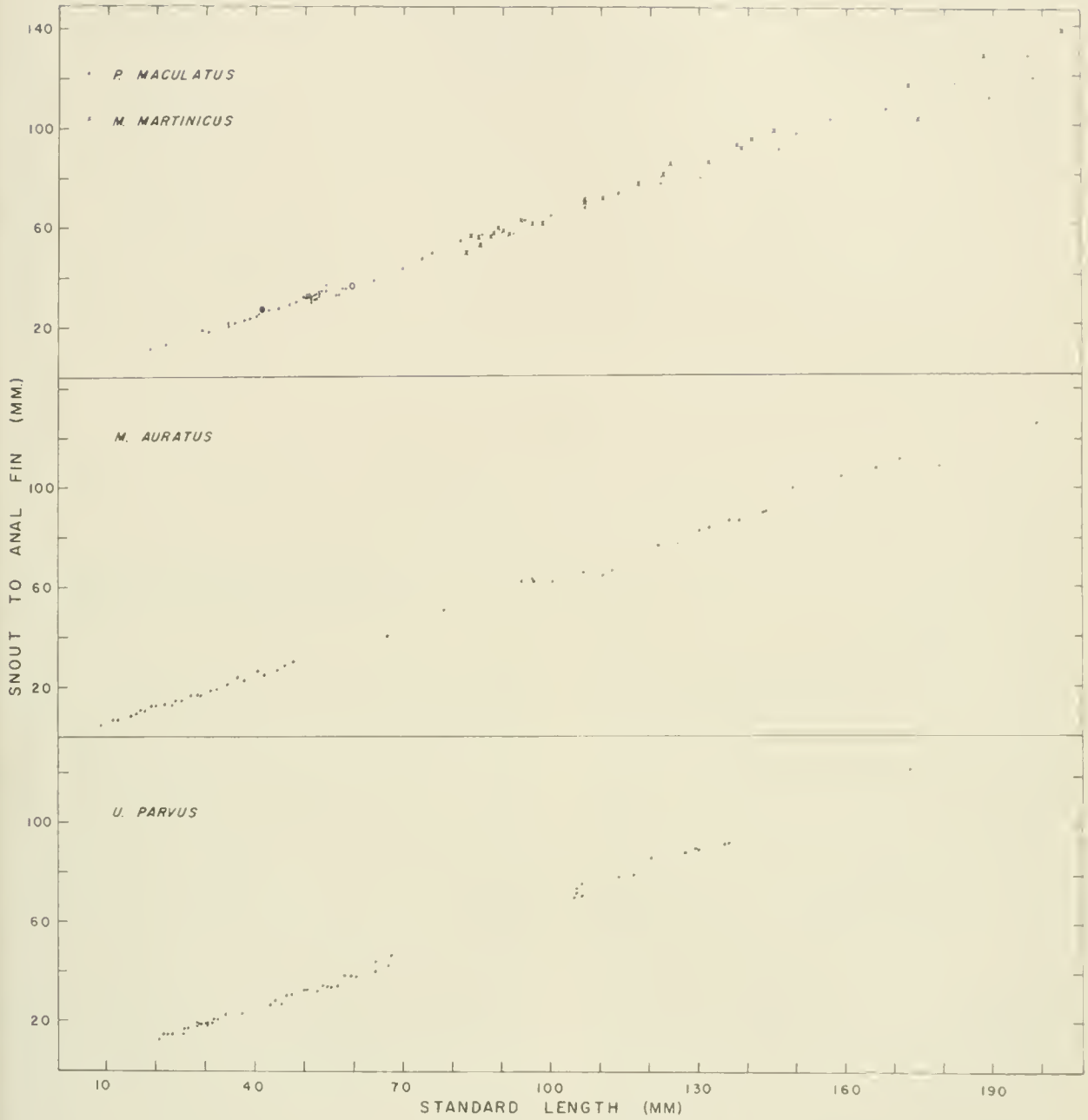

Figure 11.—Relation of distance from snout to anal fin to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

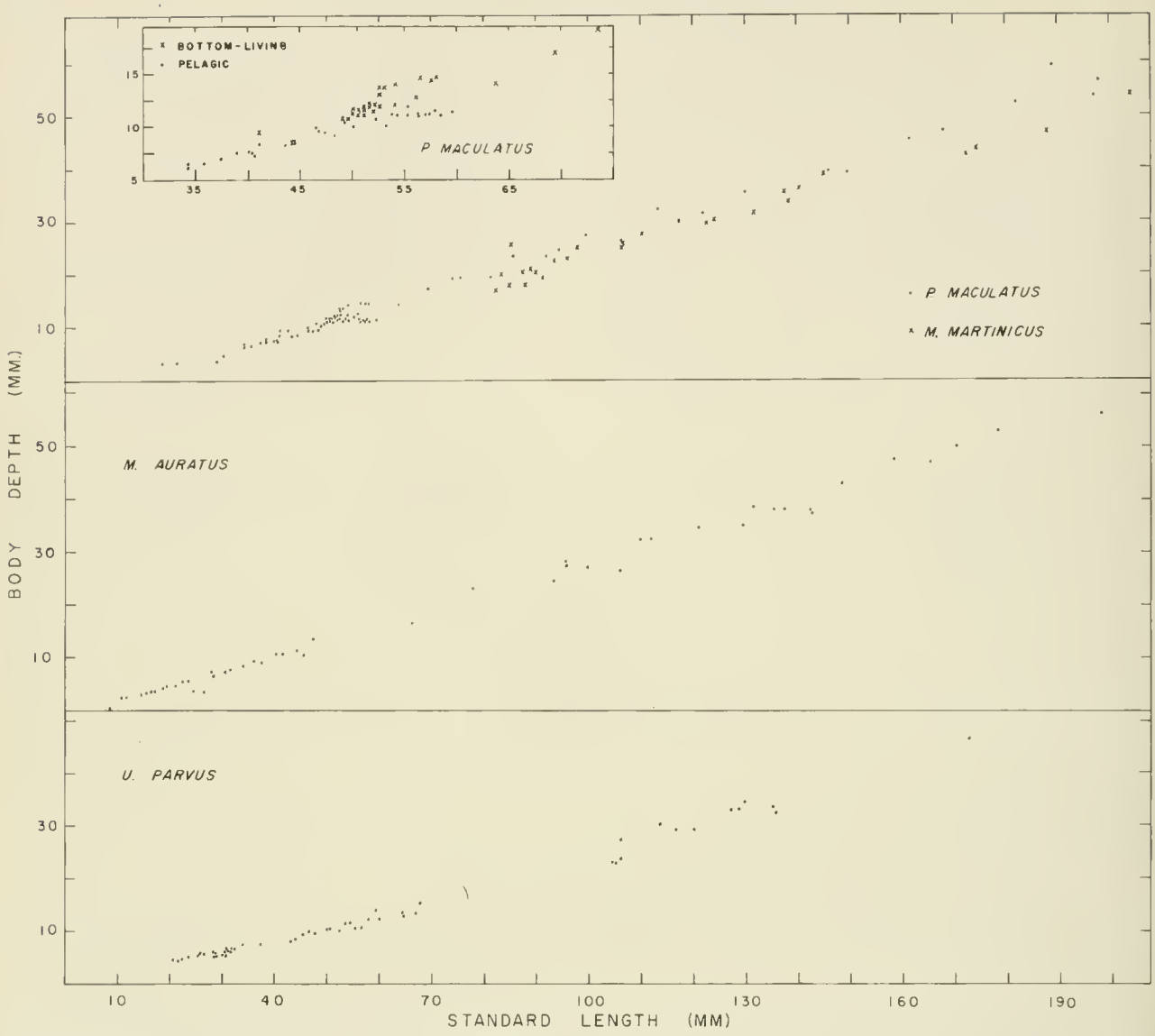

Figure 12.—Relation of body depth to standard length of Mullidae of the western North Atlantic. *Inset.* Depths of pelagic forms as opposed to depths of bottom-living forms of *Pseudupeneus maculatus.*

streaked pigment spots formed bars. These bars were directed anteriorly toward the midline at an oblique angle from the upper and lower lobes of the caudal fin, almost joining at the lateral midline to form several arrow points. Below and immediately above the lateral midline, the areas between the bars were relatively clear of pigment. Immediately below the most dorsal row of pigment spots there was additional pigmentation. In dorsal view, the body showed a single row of large, dark pigment spots along each side of the dorsal fins, which formed a long, slim "V" as the body tapered toward the caudal fin. The areas over the tip of the snout and frontal and supraoccipital bones were heavily pigmented. In ventral view, a double row of chromatophores, similar to the one on the dorsal surface, formed a "V". The fins were clear except for an occasional pigment spot on the caudal.

In a 29.0-mm. specimen the oblique bars above the lateral midline had given place to a homogeneous mottling of pigmentation. The bars below the lateral midline were still retained, the caudal and both dorsal fins had a few pigment spots, and the pelvics and anal were clear. In a 36.5-mm. specimen the oblique bars below the lat-

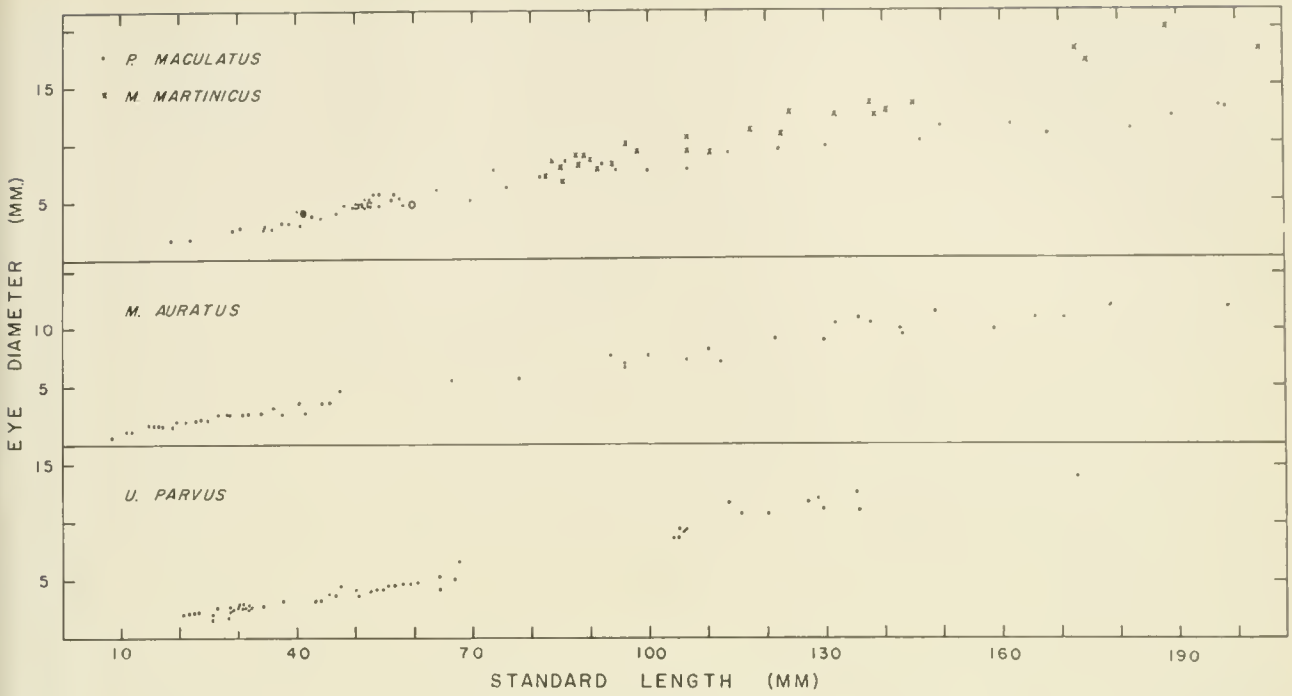

Figure 13.—Relation of eye diameter to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

eral midline were somewhat obliterated as pigmentation was more diffuse. In the lowermost pelagic specimen in figure 4, there was a clear wavy line which commenced just posterior to the tip of the opercular spine, below the lateral midline, proceeded posteriorly and parallel to the midline to a point above the tips of the pelvic rays, then turned dorsally and back anteriorly to meet the lateral midline. An enlarged mirror-image of this line was above the lateral midline, and together the two formed a heart-shaped design in which the base of the heart points anteriorly. This was typical of *P. maculatus* of this size. In the two larger specimens (fig. 4) this wavy line was elongated posteriorly. The chromatophores between the snout and the supraoccipital bones had coalesced in the 46.5-mm. (lowermost) specimen, and the two dorsal and the caudal fins had pigment spots. Chromatophores were present on the two most dorsal rays of the pectoral fins of the 50.2-mm. specimen.

A point to emphasize is that the degree of color metamorphosis in pelagic juveniles (40 to 75 mm.) does not depend upon size. A 73.5-mm. specimen in this series had about the same coloration as a 49.0-mm. specimen and lacked the black blotches that had already formed in a 41.0-mm. specimen from a different collection.

In the series of metamorphosing forms (fig. 5), the ground color was light tan. The mottling of pigment spots seen on the entire body of the pelagic specimens (fig. 4) was progressively less intense below the lateral midline of the metamorphosing forms, receding first from the ventral edge of the body. The pigmentation of the upper half of the body of the 56.5-mm. specimen (fig. 5, uppermost) was as heavy as that of the pelagic forms. The pigmentation of the fins was no different from that of the fins of the pelagic forms. No lateral black blotches have formed in any of these specimens. Pigment blotches seen in the photograph of the 56.5-mm. specimen (fig. 5) showed up better in the photograph than to the naked eye—this occurred in several instances. In this series of specimens the dark pigmentation of the lateral midline of pelagic specimens was replaced by lighter color. Slightly below the lateral midline was a second light horizontal line, apparently an extension of the lower half of the heart

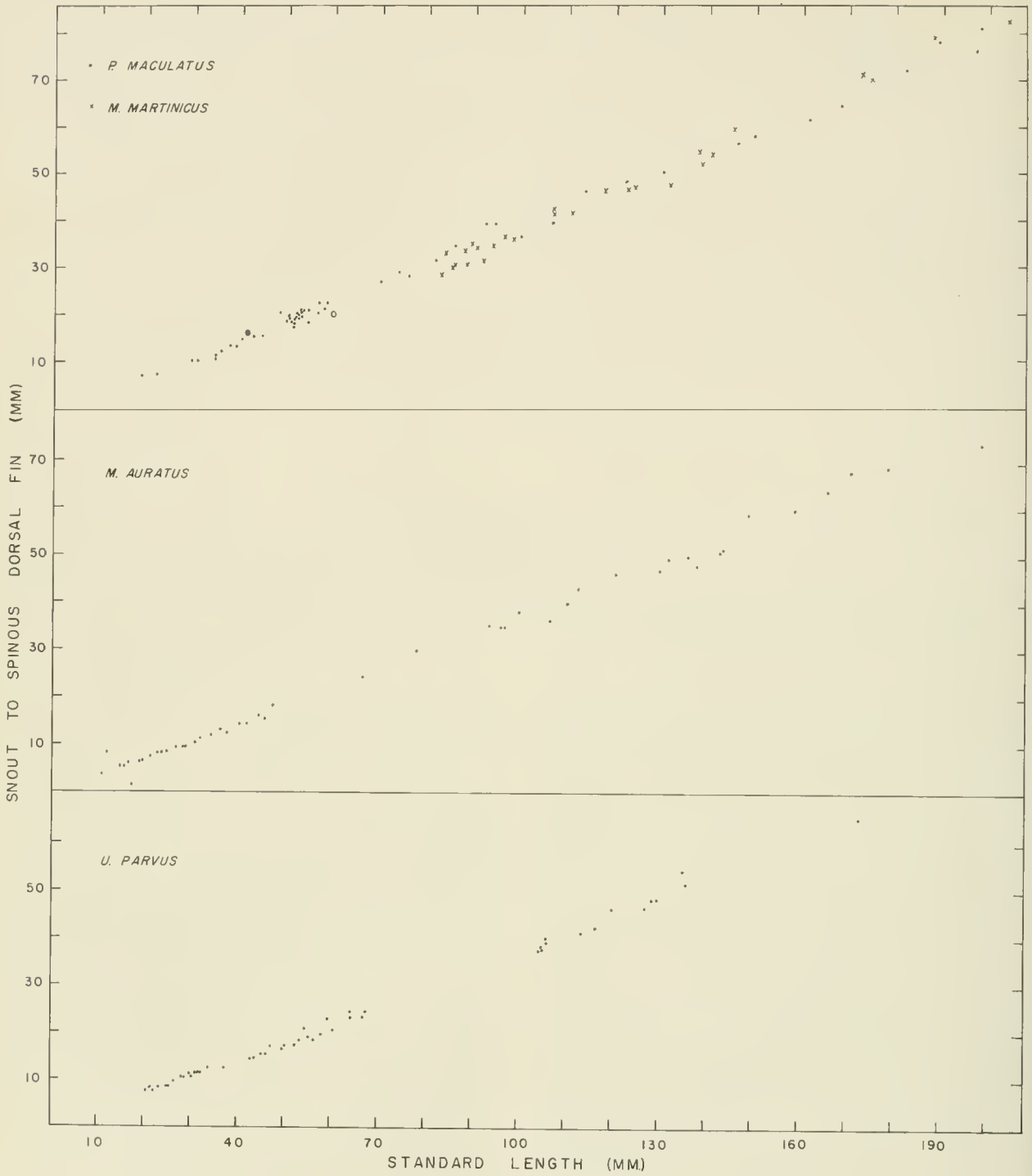

Figure 14.—Relation of distance from snout to spinous dorsal fin to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

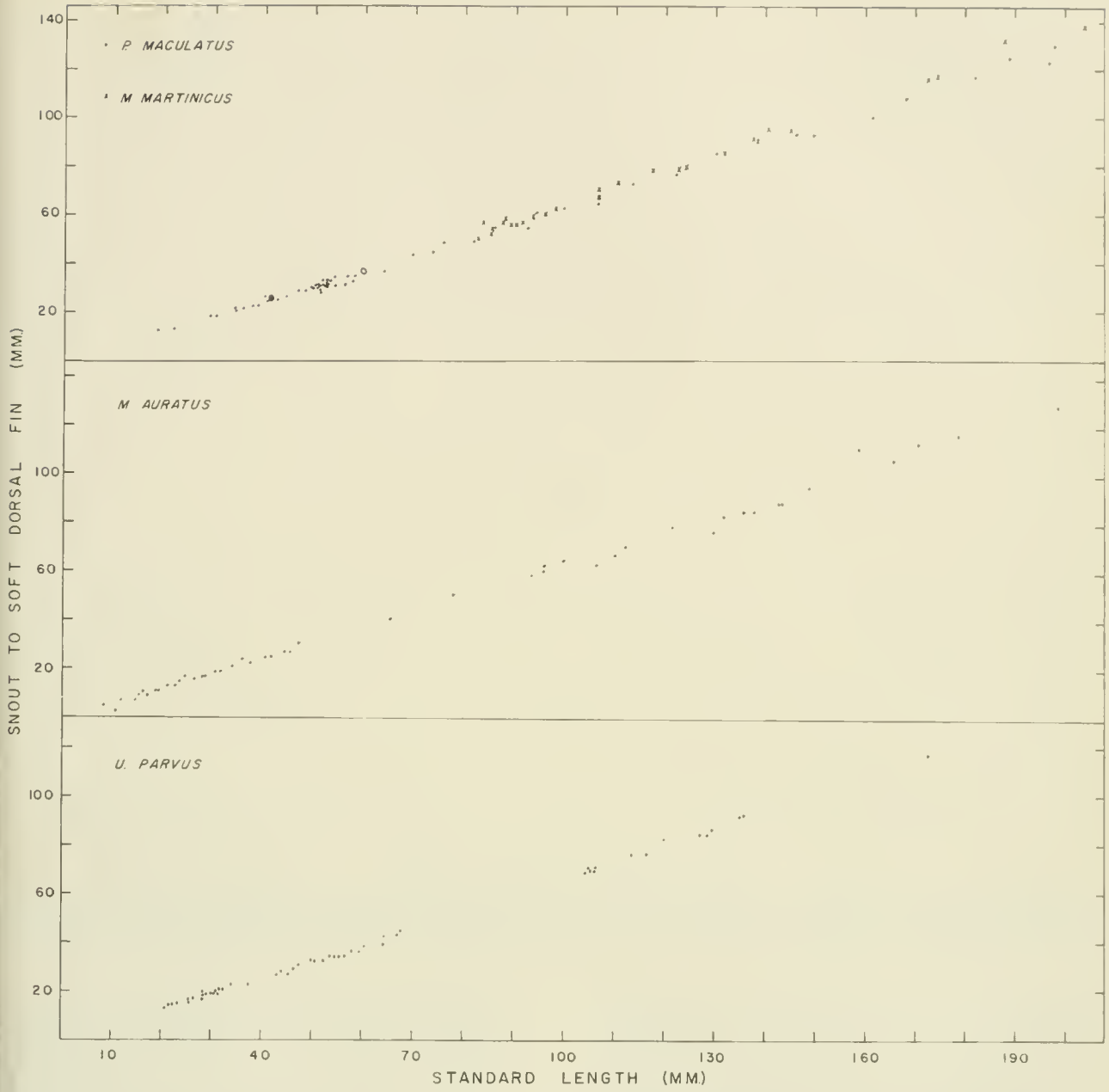

Figure 15.—Relation of distance from snout to soft dorsal fin to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

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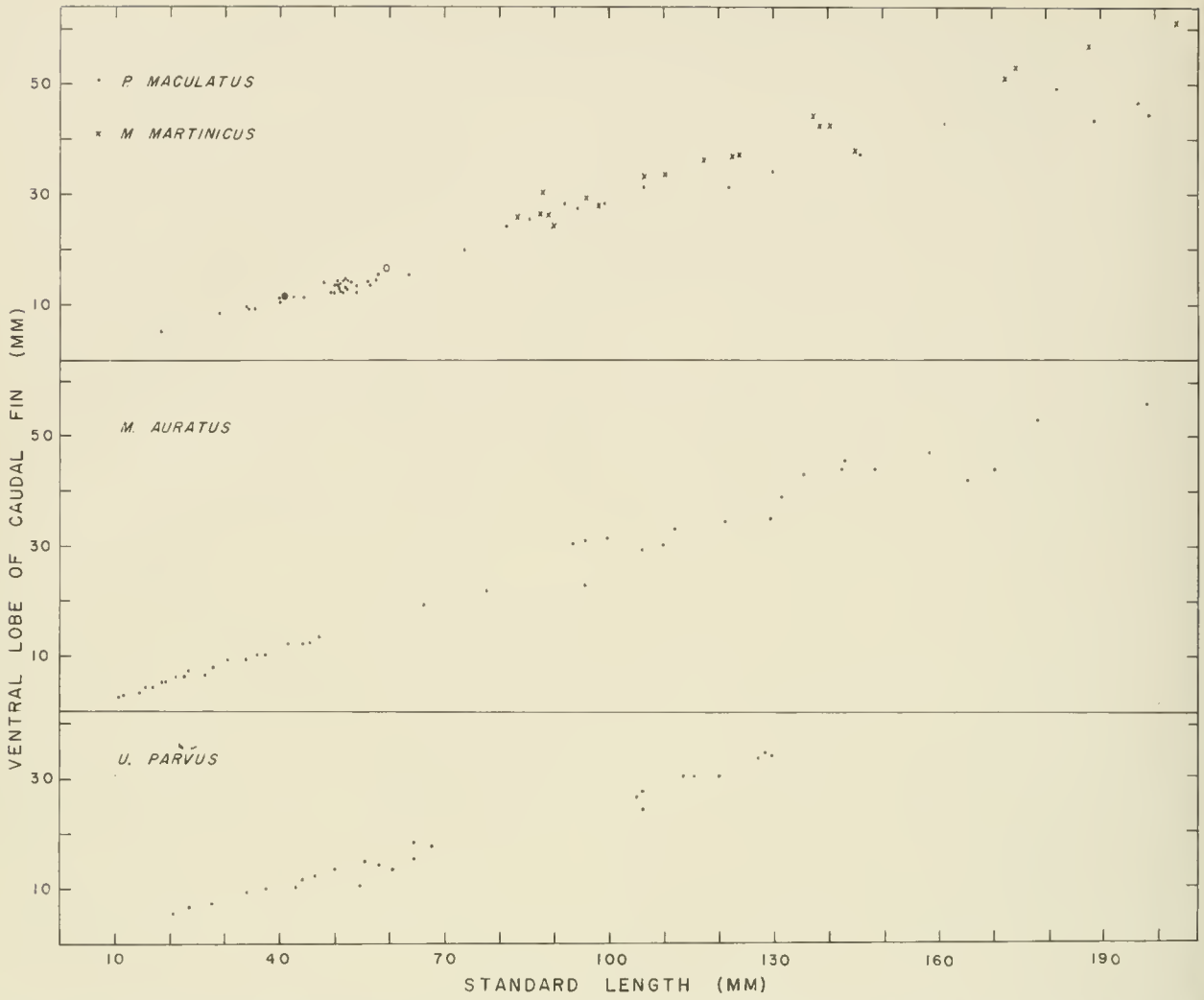

Figure 16.—Relation of length of ventral lobe of caudal fin to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

design described for pelagic juveniles. The upper half of the heart design had almost disappeared.

The black blotches that appear during metamorphosis were examined on a 94.7-mm. specimen (fig. 8). They were composed primarily of pigmentation of the scales, as there was little pigmentation of the skin. Pigmentation of the winglike process of the cleithrum occurred as the anterior blotch enlarged. At 94.7 mm. the fins had lost their pigment except for a single black patch on the second dorsal. The two light lines along the lateral midline were still obvious.

The following color description is taken from a 175-mm. adult that had been preserved in formalin for 33 days:

Body and head red. Abdomen red. Three black blotches, the first just below the lateral line at the upper edge of the operculum, the second just below the lateral line and slightly posterior to the middle of the first dorsal, and the third along the lateral line below the middle of the second dorsal. First dorsal red, second dorsal reddish-yellow, caudal red. Pectorals orange-red, pelvics red tipped with yellow. Dark streak along lateral midline—caused by coloration within the mesodermal tissue, and not by pigmentation of the scales, as are the three black patches.

Most of the pigment of the 175-mm. specimen was lost during preservation, but the three black

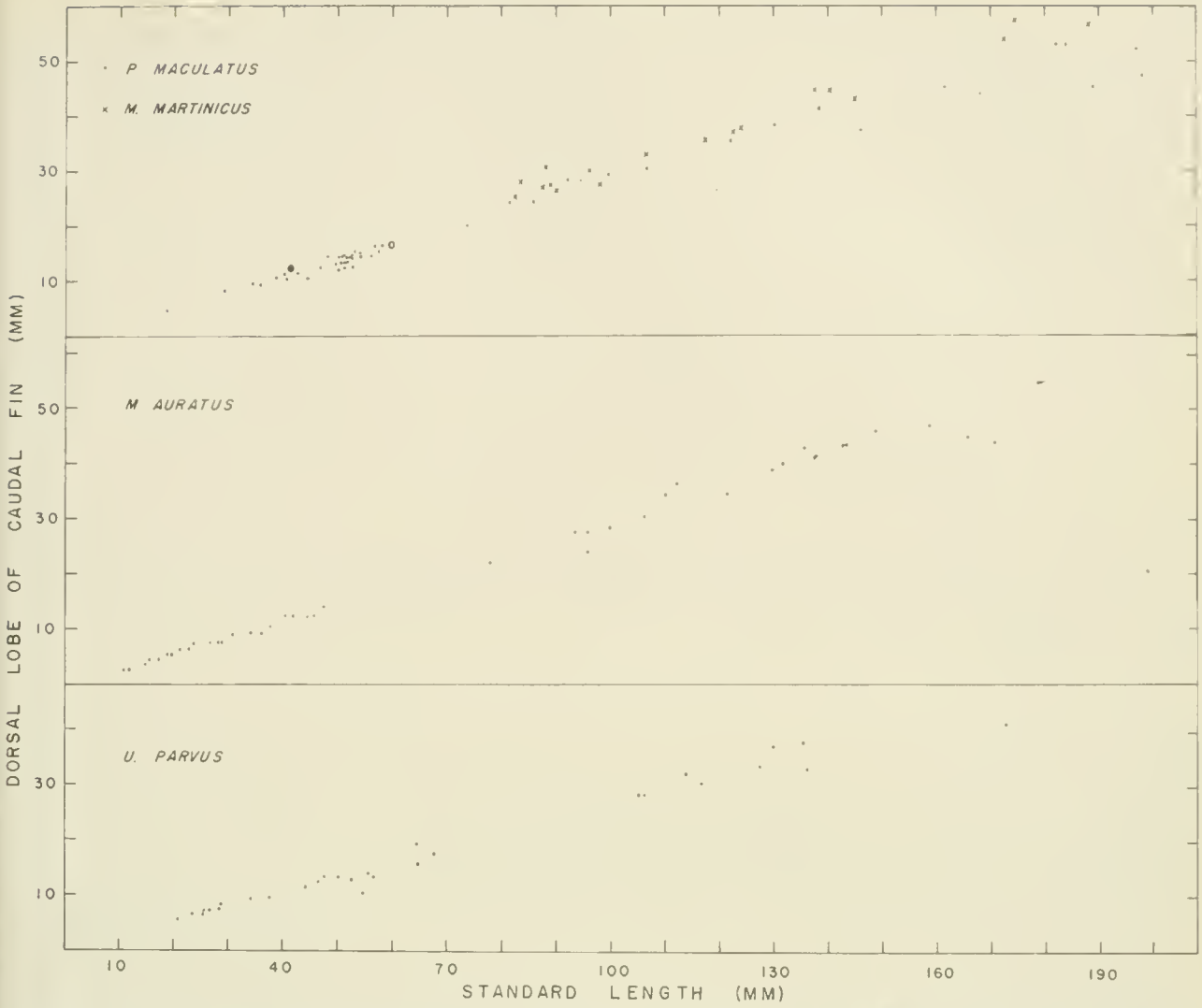

Figure 17.—Relation of length of dorsal lobe of caudal fin to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

blotches were retained (one 189-mm. specimen had four black blotches). The dark lateral midline streak was obvious on some of the preserved material.

Fins

Spinous dorsal.—All specimens had eight dorsal spines, the most anterior of which was minute (fig. 22).

Soft dorsal.—The adults had nine segmented rays, the last eight of which were branched. In the 18.5-mm. specimen, segmentation had occurred in all but the first ray. Segmentation occurred in the first ray at approximately 40 mm. In the 18.5-mm. specimen only the last ray of the soft dorsal was branched. Seven rays were branched in a 29.0-mm. specimen, and all specimens 37.4 mm. and larger had eight branched rays.

Pectoral.—Pectoral rays were counted on 56 specimens ranging from 18.5 to 197.0 mm., and the counts plotted against size ranges (table 4, p. 411). The single specimen having 13 rays on the right side, the side normally counted, had 15 on the left. All three specimens under 30.0 mm. had 15 rays. In specimens above 30 mm. there was no apparent increase in number of individuals with 16 pectoral rays over the number having 15 rays. The fin has the adult complement of rays at 40 mm.

Figure 18.—Relation of interorbital space to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

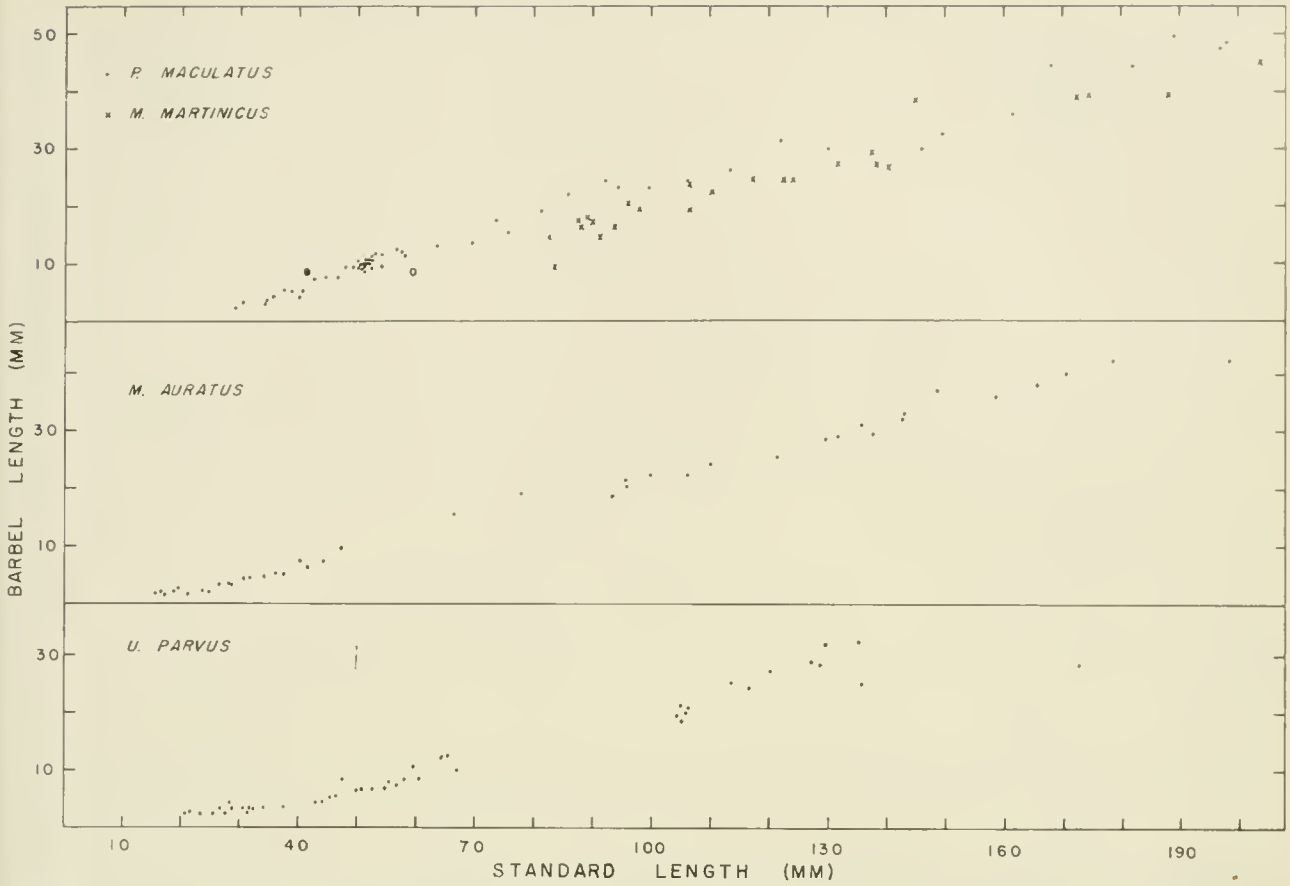

Figure 19.—Relation of barbel length to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

There were no segmented rays on 21.6-mm. or smaller specimens. In a 29.0-mm. specimen the 5th through the 11th rays were segmented. A 34.1-mm. juvenile had segmentation in the 2d through the 11th rays. A 50.2-mm. specimen with 16 rays had the 2d through the 15th rays segmented. The first ray and the last ray were not segmented on any specimens below 103.4 mm., the size at which segmentation was complete.

Branching began between 21.6 and 29.0 mm., and at 29.0 mm. the fifth ray was branched. A 34.2-mm. specimen had five branched rays, the fourth through the eighth. At 38.8 mm., the number of branched rays had increased to 10, the 3d through the 12th. At 50.2 mm., all but the first two and the last ray were branched. The last ray was not branched on any specimen below 103.5 mm., the size at which branching was complete. The first two rays never branch.

Pelvic.—In the pelvic fin of the 18.5-mm. specimen none of the six rays were branched. A 21.6-mm. specimen had two branched rays, and those 29.0 mm. and larger had five branched rays.

Anal.—The anal fin of the adult has one short spine and seven segmented rays, the last six branched. The seven rays were segmented in an 18.5-mm. specimen, but only the last two were branched. At 29.0-mm. the last six rays were branched.

Caudal.—The principal ray count on all specimens was 15 (i, 7+6, i). Secondary ray counts were made on 12 specimens ranging from 18.5 through 57.5 mm. In specimens larger than this the secondary rays are so overgrown by tissue and scales that counts were unreliable. The secondary ray counts ranged from 8 to 10 in the dorsal lobe and 8 to 11 in the ventral lobe. The smallest specimen had 9 dorsal and 10 ventral secondary

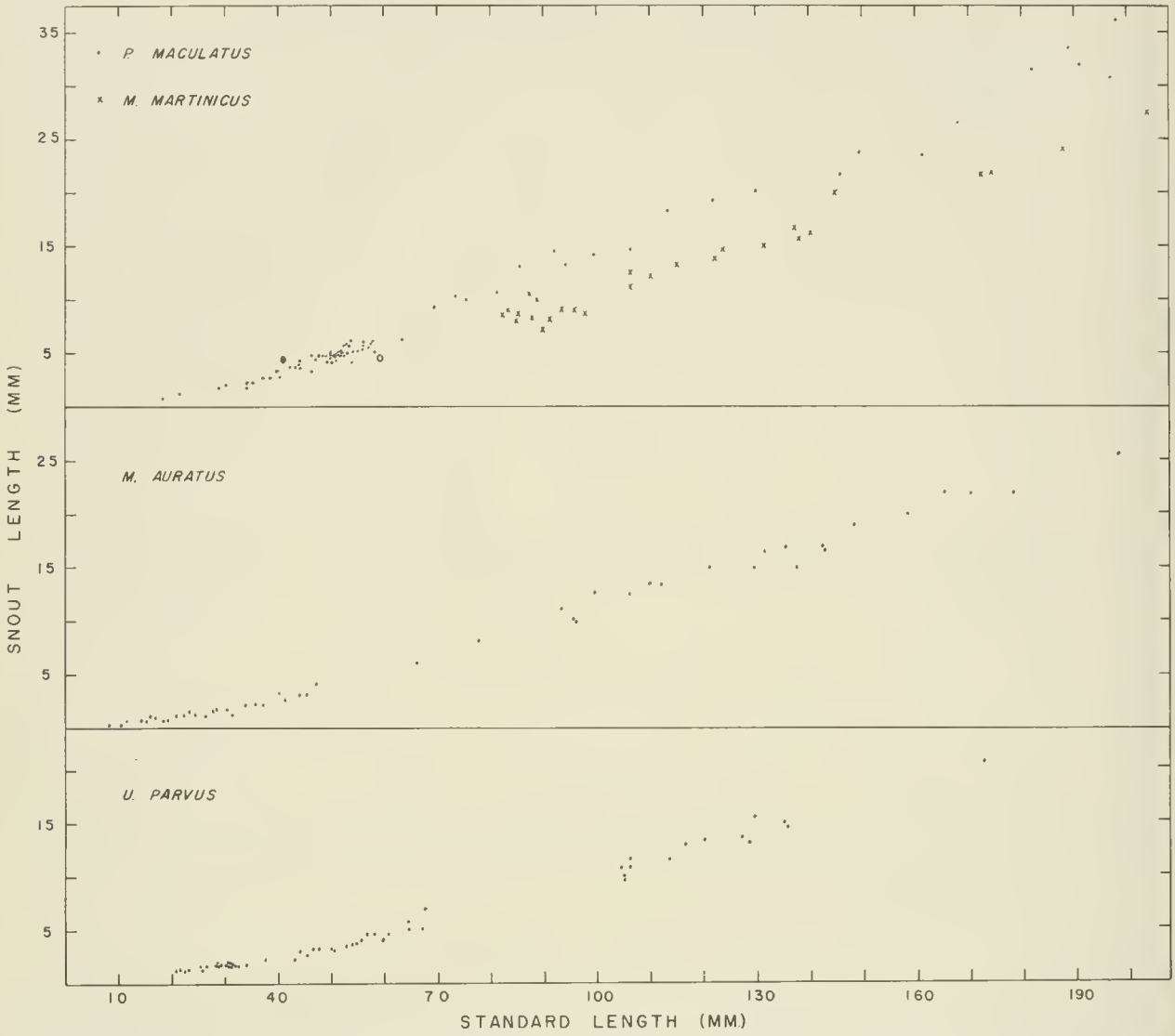

Figure 20.—Relation of snout length to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

rays, and was considered a juvenile. On both dorsal and ventral caudal lobes, the secondary ray adjacent to the principal rays was segmented. A 57.5-mm. specimen had the first two rays adjacent to the principal rays segmented. The cleared and stained caudal fin of a 178-mm. specimen showed no additional segmentation of either lobe beyond those first two secondary rays adjacent to the principal rays.

Gill rakers

Total.—Total number of gill rakers was counted on 60 specimens. The number of upper-limb gill rakers on two smaller specimens (18.5 and 21.6 mm.) was indeterminate, and the specimens were not available for staining. From 29.0 to 198.0 mm. the total number of gill rakers ranged from 26 to 32, with the exception of one specimen (34.2 mm.) which had 24.

When plotted against total body length ranges (table 5, p. 411), the total number of gill rakers averaged highest in the size range from 50.0 to 74.9 mm. There was a decrease after this size as the gill rakers farthermost from the angle of the arch become overgrown with tissue.

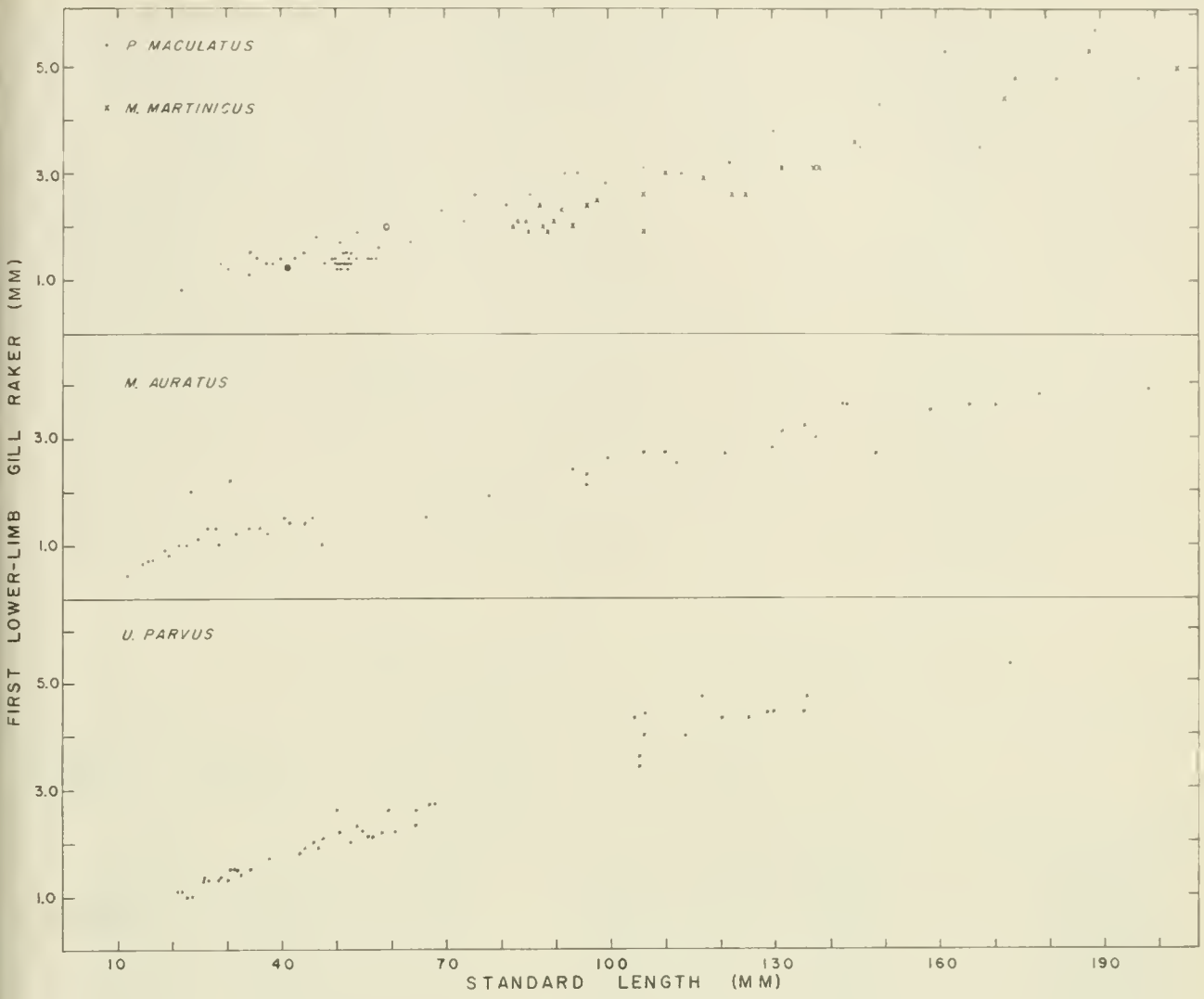

Figure 21.—Relation of length of first lower-limb gill raker to standard length of Mullidae of the western North Atlantic. For *Pseudupeneus maculatus*, large black circle indicates smallest metamorphosed specimen (41.0 mm.) and large open circle indicates large pelagic form (59.5 mm.).

Lower limb.—The lower-limb gill rakers were counted on these 60 specimens as well as the two smaller specimens mentioned above. The number of lower-limb gill rakers ranged from 19 to 24, with the exception of 1 specimen (21.6 mm.) which had 17 (table 6, p. 428).

The average number increased with size up through a 50.0- to 74.9-mm. size range, then decreased as the rudiments became overgrown with tissue.

Ceratobranchial bone.—The number of gill rakers on the ceratobranchial bone was counted on 32 specimens. Of these, 2 (18.5 and 34.2 mm.) had 11, 1 had 15 (85.8 mm.), and the remainder had from 12 to 14.

Teeth

Upper jaw.—Among the Mullidae of the western North Atlantic, curved canines in the upper jaw anterior and lateral to the main row of canines are peculiar to *P. maculatus*. Teeth were not evident in an 18.5-mm. specimen, but were present in one of 21.6 mm. The left premaxillary bone of a 46-mm. specimen had a regular series of 14 erupted canine teeth, plus 6 unerupted teeth in the 6th, 8th, 10th, 14th, 17th, and 19th positions from

TABLE 6.—*Relation of numbers of lower-limb gill rakers (exclusive of one at angle of arch) to standard length of 62 specimens of* Pseudupeneus maculatus

[The upper number is the number of specimens, and the number in parentheses below is the approximate percentage for the respective size range]

Standard length (mm.)	Number of lower-limb gill rakers								Number of specimens
	17	18	19	20	21	22	23	24	
0–19.9				1 (100)					1
20.0–29.9	1 (50.0)			1 (50.0)					2
30.0–39.9			2 (33.3)	2 (33.3)	2 (33.3)				6
40.0–49.9				3 (37.5)	3 (37.5)	2 (25.0)			8
50.0–74.9			1 (3.6)	2 (7.1)	5 (17.9)	12 (42.9)	5 (17.9)	3 (10.7)	28
75.0–99.9			1 (16.7)	3 (50.0)	2 (33.3)				6
100.0–124.5			1 (33.3)	1 (33.3)		1 (33.3)			3
125.0–149.5			2 (66.7)		1 (33.3)				3
150.0–200.0			2 (40.0)	2 (40.0)	1 (20.0)				5

TABLE 7.—*Collection and station data for 587 specimens of* Mullus auratus *examined*

[Dip net (D), trawl (T), and stomach contents (SC)]

Station	Latitude	Longitude	Date of capture	Depth of water in which captured	Method of capture	Number of specimens and size range	Collection and catalogue number (if any)
WESTERN NORTH ATLANTIC:				*Fathoms*		*mm.*	
Gill Cr. 2, Reg. 76	34°53′ N.	76°10′ W.	May 11, 1953	8	D	(4) 25.5–39.0	BLBG
Silver Bay 1267	34°35′ N.	75°55′ W.	Sept. 11, 1959	24	T	(47) 100.0–126.0	BLBG
Silver Bay 1269	34°32′ N.	75°57′ W.	Sept. 12, 1959	25	T	(26) 94.0–128.5	BLBG
Silver Bay 1268	34°32′ N.	75°53′ W.	Sept. 11, 1959	30–31	T	(2) 114.5 and 117.0	BLBG
Silver Bay 1299	34°21′ N.	76°34′ W.	Sept. 23, 1959	14	T	(7) 108.0–121.0	BLBG
Gill Cr. 1, Reg. 73	34°09′ N.	75°22′ W.	Mar. 6, 1953	[1] 1500	D	(1) 16.0	BLBG
Silver Bay 1214	34°02′ N.	77°35′ W.	Sept. 3, 1959	11	T	(2) 181.5 and 202.5	BLBG
Silver Bay 1215	33°56′ N.	77°20′ W.	Sept. 3, 1959	15	T	(1) 197.5	BLBG
Silver Bay 1508	33°49′ N.	77°27′ W.	Dec. 9, 1959	18	T	(1) 150.5	BLBG
Silver Bay 1209	33°41′ N.	77°40′ W.	Sept. 2, 1959	11–12	T	(2) 117.5 and 134.5	BLBG
Silver Bay 1692	33°21′ N.	77°17′ W.	Feb. 28, 1960	25–26	T	(1) 149.0	BLBG
Silver Bay 1204	33°21′ N.	77°24′ W.	Sept. 1, 1959	15–16	T	(4) 109.0–128.0	BLBG
Silver Bay 1349	33°18′ N.	78°44′ W.	Oct. 19, 1959	9	T	(1) 131.0	BLBG
Silver Bay 1673	33°14′ N.	77°41′ W.	Feb. 27, 1960	18–19	T	(1) 163.0	BLBG
Silver Bay 1354	33°06′ N.	78°46′ W.	Oct. 19, 1959	11	T	(1) 117.0	BLBG
Silver Bay 1361	33°00′ N.	78°40′ W.	Oct. 20, 1959	15–16	T	(5) 118.0–126.5	BLBG
Silver Bay 1733	33°00′ N.	78°26′ W.	Mar. 7, 1960	17	T	(1) 159.0	BLBG
Silver Bay 1358	32°58′ N.	78°13′ W.	Oct. 20, 1959	23–24	T	(1) 134.5	BLBG
Silver Bay 1364	32°54′ N.	79°12′ W.	Oct. 21, 1959	11	T	(5) 117.5–128.5	BLBG
Silver Bay 1734	32°51′ N.	78°39′ W.	Mar. 7, 1960	17	T	(1) 166.5	BLBG
DeVeaux's Bank, vicinity of Charleston, S.C.					SC	(1) 96.0 [2]	ChM 31.150.6
S.E. of Edisto River Sea Buoy, vicinity of Charleston, S.C.			Feb. 24, 1958	18		(1) 143.0	ChM 58.2.11
Silver Bay 1359	32°45′ N.	78°23′ W.	Oct. 20, 1959	50	T	(1) 134.0	BLBG
Silver Bay 1742	32°41′ N.	78°27′ W.	Mar. 8, 1960	45–68	T	(8) 129.0–165.0	BLBG
Combat 299	32°22′ N.	78°14′ W.	Apr. 21, 1957	250	D?	(9) 15.0–29.0	BLBG
Combat 428	32°17′ N.	79°10′ W.	June 25, 1957	24–28	T	(1) 66.5	UMIM 1972
Gill Cr. 2, Reg. 49	32°12′ N.	78°25′ W.	May 7, 1953	185	D	(14) 24.0–37.5	BLBG
Gill Cr. 2, Reg. 43	32°12′ N.	79°33′ W.	May 6, 1953	17	D	(3) 21.5–29.0	BLBG
Silver Bay 1754	32°06′ N.	79°11′ W.	Mar. 9, 1960	49–50	T	(2) 170.0 and 174.5	BLBG
Gill Cr. 2, Reg. 42	31°57′ N.	79°18′ W.	May 6, 1953	75	D	(16) 19.0–33.0	BLBG
Gill Cr. 2, Reg. 36	31°42′ N.	80°38′ W.	May 5, 1953	12	D	(1) 17.5	BLBG
Gill Cr. 2, Reg. 31	31°00′ N.	79°59′ W.	April 28, 1953	28	D	(2) 15.0 and 18.0	BLBG
Silver Bay 1621	30°48′ N.	80°29′ W.	Jan. 28, 1960	20	T	(1) 155.0	BLBG
Gill Cr. 2, Reg. 25	30°20′ N.	80°35′ W.	Apr. 27, 1953	18	D	(4) 17.5–25.0	BLBG
Silver Bay 2084	29°53′ N.	80°34′ W.	May 5, 1960	21	T	(2) 145.0 and 159.0	BLBG
Gill Cr. 2, Reg. 20–21	29°40′ N.	80°57′ W.	Apr. 26, 1953	9	D	(13) 34.5–39.0	BLBG
Gill Cr. 2, Reg. 19	29°39′ N.	80°23′ W.	Apr. 26, 1953	23	D	(2) 37.5 and 38.0	BLBG
Silver Bay 460	29°38′ N.	80°14′ W.	June 13, 1958	75	T	(1) 138.0	BLBG
Combat 488	29°30′ N.	80°13′ W.	Aug. 19, 1957	50	T	(3) 132.0–147.0	BLBG
Combat 350	29°27′ N.	80°20′ W.	June 3, 1957	28	T	(1) 131.0	BLBG
Combat 339	29°19′ N.	80°18′ W.	June 1, 1957	25	T	(3) 136.0–168.0	BLBG
Combat 335	29°03′ N.	80°13′ W.	June 1, 1957	28	T	(1) 171.0	BLBG

See footnotes at end of table.

TABLE 7.—*Collection and station data for 587 specimens of* Mullus auratus *examined*—Continued

[Dip net (D), trawl (T), and stomach contents (SC)]

Station	Latitude	Longitude	Date of capture	Depth of water in which captured	Method of capture	Number of specimens and size range	Collection and catalogue number (if any)
				Fathoms		*mm.*	
WESTERN NORTH ATLANTIC—Con.							
Combat 334	29°15′ N.	80°13′ W.	June 1, 1957	30	T	(1) 125.0	BLBG
Gill Cr. 2, Reg. 13	29°00′ N.	80°33′ W.	Apr. 25, 1953	9	D	(15) 23.5-39.5	BLBG
Gill Cr. 6, Reg. 10	28°20′ N.	80°10′ W.	Apr. 27, 1954	21	D	(1) 28.0	BLBG
Gill Cr. 5, Reg. 6	27°40′ N.	79°41′ W.	Jan. 31, 1954	260	D	(3) 18.0-22.0	BLBG
Gill Cr. 6, Reg. 4	27°20′ N.	80°04′ W.	Apr. 26, 1954	13	D	(25) 28.0-41.0	BLBG
Gill Cr. 2, Reg. 3	27°01′ N.	80°01′ W.	Apr. 23, 1953	6	D	(145) 8.0-42.0	BLBG
GULF OF MEXICO:							
Pompano 5, 14 mi. west of Charlotte Harbor, Fla.			Apr. 21, 1949	10		(1) 40.0	BLBG
Ellen, Sea Horse Reef, Fla.			June 19, 1949		T	(1) 47.5	UMIM 3105
Oregon 2159	28°03′ N.	83°20′ W.	Apr. 9, 1958	21	D	(6) 22.0-39.5	BLBG
Oregon 602	29°32′ N.	86°21′ W.	July 12, 1952	80	T	(2) 134.0 and 163.0	TU 6067
Oregon 1095	27°10′ N.	96°17′ W.	June 5, 1954	175	T	(1) 149.0	TU 12890
Oregon 1081	26°10′ N.	96°59′ W.	June 2, 1954	15	T	(1) 78.5	UF
Oregon 2470	20°12′ N.	91°59′ W.	Apr. 14, 1959	10	D	(1) 43.0	USFWS Ichth. Lab.
Silver Bay 403	22°12′ N.	89°57′ W.	May 11, 1958	27	D	(170) 12.0-46.0	BLBG
Silver Bay 410	22°13′ N.	89°50′ W.	May 12, 1958	27	D	(1) 40.0	BLBG
Oregon 2174	22°23′ N.	89°44′ W.	May 11-12, 1958	15	D	(9) 40.0-45.0	USFWS Ichth. Lab.
Silver Bay 411	22°11′ N.	88°53′ W.	May 14, 1958	23	T	(2) 156.0 and 173.0	BLBG

[1] Estimated from hydrographic chart. [2] Regurgitated by young royal tern.

TABLE 8.—*Relation of size of specimen, method of capture (dip net, D; trawl, T), and water depths in which captured for* Mullus auratus

[Each letter represents a capture of one or more specimens within a particular size range]

DEPTH IN FATHOMS	SIZE RANGE IN MILLIMETERS				
	0–24.5	25.0–49.5	50.0–74.5	75.0–99.5	Over 100
Over 100	DDD	DDDD			T
75–99	D	D			TT
50–74					T
25–49	DD	DDD	T	T	TTTT TTTT
0–24	DDDD DD	DDDD DDDD DDDD D			TTTT TTTT TTTT TTTT TTTT

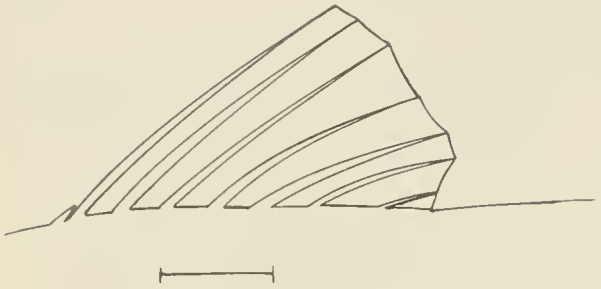

Figure 22.—Spinous dorsal fin of 46.0-mm. *Pseudupeneus maculatus*. Line equals 2 mm.

the anterior end of the premaxilla. None of the unerupted teeth was out of position in the series, and those that had erupted curved somewhat toward the back of the mouth. The right premaxillary had 19 erupted teeth and 2 unerupted teeth toward the back of the jaw, an adult complement of teeth in the main row.

The left premaxillary bone of a 94.8-mm. specimen had a regular series of 14 inwardly curved canine teeth plus sockets containing undeveloped teeth in the fourth and ninth positions. The right premaxillary was similar but had in addition a larger canine, in the fourth position in the regular row, directed toward the right side of the month and curved upward. This single, larger, backwardly curving canine anterior to the regular series was not apparent in any specimen under 79.2 mm. Of the specimens examined for this character, it was present in 25 percent of those 80 to 100 mm., 50 percent of those 100 to 130 mm., and 90 percent of those over 130 mm. This tooth either forms in addition to the regular series, or is one that enlarges, becomes hooked, and migrates to a position anterior to the others in the regular row of teeth.

A 108.0-mm. specimen did not have the large canine seen on the 94.8-mm. specimen. The left premaxillary bone had a row containing 19 evenly spaced, fully developed teeth and two unerupted teeth in the 16th and 19th tooth sockets. The right premaxillary had a developing tooth and socket at the base of the second tooth in addition to the regular series of erupted and erupting teeth.

The upper jaw of a 119.5-mm. specimen had a row of canines which were for the most part curved down and toward the back of the mouth.

The two front teeth curved toward each other and the back of the mouth. Anterolateral to these on each of the premaxillaries was a large canine which curved anteriorly and outward. Set slightly above the regular series of teeth, the one in the right premaxillary was between the fourth and fifth teeth, and the one on the left was between the third and fourth teeth. Medial to the two oversized teeth, and set above and between the bases of the second and third teeth in the regular row, were large sockets each containing a developing tooth much larger than those in the regular series. These pointed toward the floor of the mouth. A second oversized canine was found above, anterior to, and in addition to the regular series. This second oversized canine had not erupted on any specimen examined smaller than 115 mm. and was seen on 50 percent of the specimens over this size.

A 146-mm. specimen had, anterior to the regular row, a third large canine on each premaxillary bone. These were medial to the other two and curved toward each other and upward. Noticed on 20 percent of the larger specimens, this third canine sometimes appeared on only one of the premaxilliaries.

I examined only two specimens over 200 mm., one 206 mm., the other 225 mm., and each had the additional curved canines. Three was the maximum number found on either half of the premaxillary.

Lower jaw.—Teeth were not evident in an 18.5-mm. *P. maculatus*, but were visible in all specimens 21.6 mm. and larger. A 49-mm. specimen had 12 and 13 canine teeth in a single row on the left and right dentaries respectively.

Vomerine and palatine.—No teeth were seen on the vomerine or palatine bones of any specimen of *P. maculatus*.

Scales

Lateral line scales were counted on 41 specimens ranging from 41.0 to 197.0 mm. The counts ranged from 27 to 31 with the two extremes being encountered only once (2.4 percent). The other counts were 28 (46.3 percent), 29 (29.3 percent), and 30 (19.5 percent). Specimens up through a size of 38.8 mm. had either no scales (18.5 mm.) or only a few along the dorsal and ventral surfaces concentrated in the regions of the dorsal and anal fins, and one large scale in the axilla of the pectoral (21.6 through 38.8 mm.). Whereas it is possible that scales do not develop except in these regions before a size of approximately 40 mm., the fact

that a 41.0-mm. metamorphosed specimen had an adult complement of 30 firmly fixed lateral line scales makes this unlikely.

A 30.1-mm. specimen had no ctenii on the scales, but a 42.4-mm. specimen had 18 ctenii on one of the scales. These ctenii appear to be set into marginal sockets. The ctenii had increased to 52 in a 50.2-mm. specimen and 141 in a 189.0 mm. specimen. The ctenii of the scales of the 189.0-mm. specimen had changed in appearance so that they resembled sharply pointed cells protruding from the margin of the scale, the outermost of a series of other cell-like structures, rectangular in shape.

Barbels

In an 18.5-mm. specimen both barbels were free from the branchiostegal membrane except at the tip of the right barbel. In a 21.6-mm. specimen, neither barbel was free, but had separated at the base. Both barbels were free at 29.0 mm. and larger sizes.

Operculum

The adult has a strong opercular spine at about the anterior end of the lateral midline. There was no evidence of this spine on an 18.5-mm. specimen. It was noted on a specimen of 21.6 mm., but the tip did not extend to the margin of the operculum. On a 29.0-mm. specimen it was clearly seen, as it was on all larger specimens examined. A second small spine, anterior to the large spine, was noted on an occasional large specimen.

Cleithrum

The cleithrum had an enlarged winglike process just posterior to the upper angle of the opercular flap. It had a remarkable resemblance to a scale as it acquired the pigmentation occurring as a dark blotch in this region. At a size of approximately 40 mm., the same size at which the scales become ctenoid, this small prominent bone had serrations, further increasing its similarity to a ctenoid scale. At sizes above 50 mm. this serrated cleithral wing was the quickest and easiest method of identifying *P. maculatus*, as this character is peculiar to this species of the Mullidae of the western North Atlantic.

The upper wing of the cleithrum of a 46.0-mm. juvenile and its position relative to the operculum and opercular spine are illustrated (fig. 23).

Figure 23.—Operculum and cleithrum of 46.0-mm. *Pseudupeneus maculatus*. Line equals 2 mm.

SPAWNING

Forty-mm. specimens taken as early as January 1 and as late as July 25 (table 2) suggest a protracted spawning period.

SEXUAL DIMORPHISM

Eight large, mature *P. maculatus*, four 190.0- to 206.0-mm. males and four 165.0- to 181.0-mm. females, were examined for sexual dimorphism. The males tended to have higher arched backs and more angular facial profiles, whereas the females tended to be more fusiform and have a sloping facial profile. The angulation of the profile and arched back of the male was more pronounced with increase in size.

The 197.0-mm. specimen plotted on the graphs of body proportions (figs. 9 through 21) is a female, and the 198.0-mm. specimen is a male. These two specimens, the most extreme of the ones examined, illustrate sexual dimorphism for this species.

MULLUS AURATUS JORDAN AND GILBERT

Pertinent station data and sources of material are given in table 7, p. 429.

DISTRIBUTION

Briggs (1958) listed the range of *Mullus auratus* as Bermuda and Nova Scotia to the West Indies and throughout the Gulf of Mexico. All of my specimens (table 7) fall within this range, and their locations of capture are shown in figure 24.

ECOLOGY

A pelagic larval existence is suggested for *M. auratus* by the capture of the young up to 46 mm. by dip net only. Specimens 47.2 mm. and larger were taken by bottom trawl (table 8, p. 429).

The larval and premetamorphosed juveniles were, for the most part, preserved in formalin and ranged in color from dark to medium brown. The metamorphosed juveniles and adults were tan, yellowish, or red, depending on the length of time that they had been preserved, and had many varicolored stripes on their fins (stripes disappear with preservation).

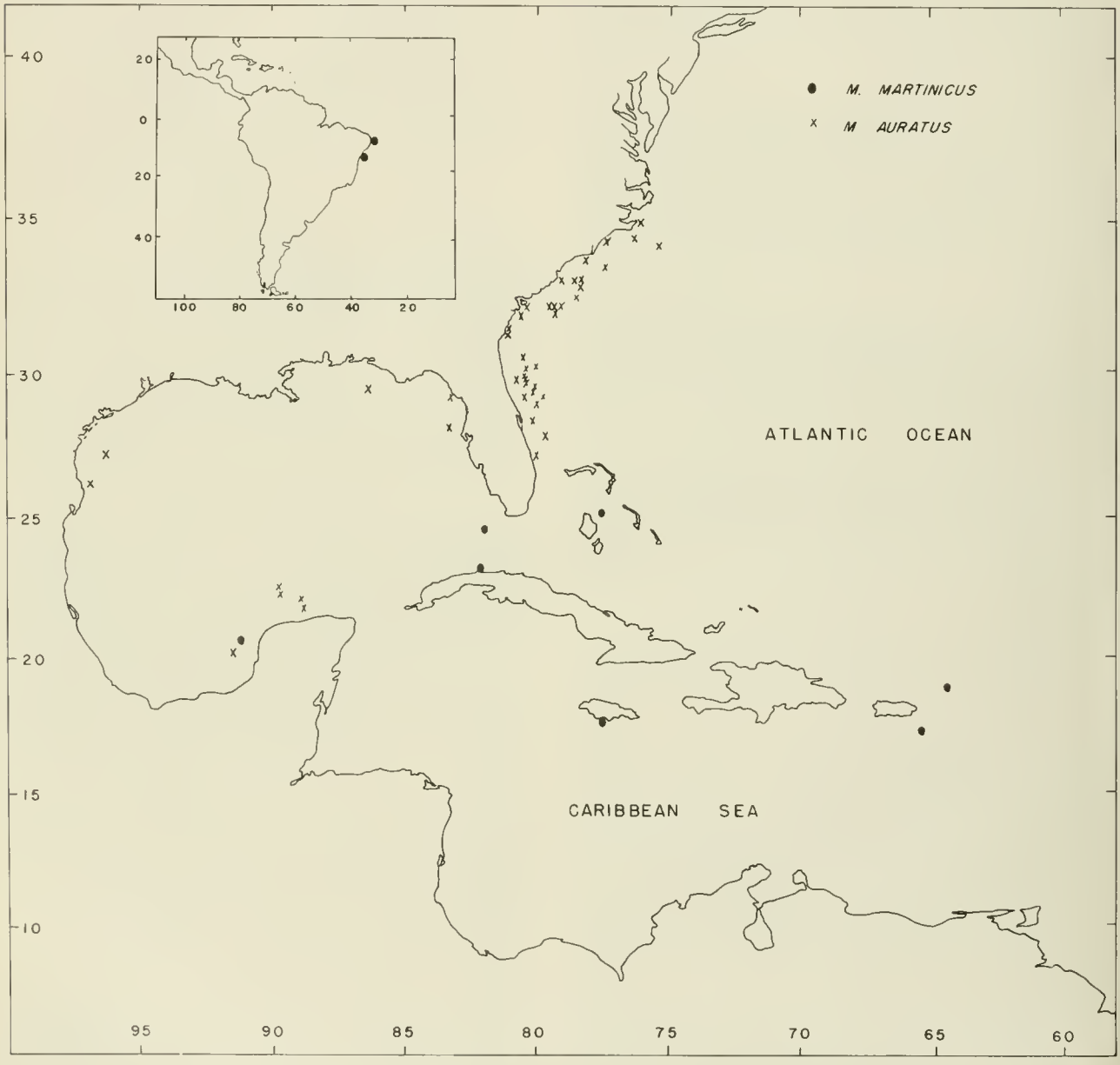

Figure 24.—Locations of capture of *Mullus auratus* and *Mulloidichthys martinicus*.

As young *M. auratus* were taken in numbers by dip net through 46 mm., but all specimens 47.2 mm. and larger were taken only by bottom trawl (table 8), it appears that the species can terminate its pelagic existence and descend to the bottom when it reaches a size of approximately 45 mm. It was at this size that the species changed markedly in appearance, as shown in the photograph (fig. 25), in which the upper fish is a 47.2-mm. specimen taken at Seahorse Reef (Cedar Keys), Fla., by trawl; the lower fish is a pelagic 45.8-mm. specimen dip netted off Yucatan. This metamorphosing 47.2-mm. *M. auratus* was the only specimen in the size range from 46 to 66 mm. available for examination, and it was the only specimen with which a direct comparison could be made with a pelagic form of similar size. However, on the basis of this one specimen, *M. auratus* does undergo a metamorphosis, but the change of appearance is not so marked as in *P. maculatus*. The graphs of body dimensions for *M. auratus* (figs. 9 through 21) do not indicate marked or abrupt changes in dimensions at 45 mm. except in snout length and head length, but these might become evident if more specimens of the size 50-70 mm. were examined (see Body Proportions, *M. auratus*).

No juveniles were taken in the deeper waters of the Gulf of Mexico in spite of the thorough work by the U.S. Fish and Wildlife Service vessels in this area in recent years. This could indicate either that juveniles prefer shallower waters or that the adults do not spawn in or close to deep water. Some small specimens were taken off the Atlantic coast in deep water, but a comparison of the water depths at locations of capture of the three species on which I have comparative data (tables 2, 7; and 12, p. 435) shows that those depths for *P. maculatus* and *U. parvus* tend to be greater than those for *M. auratus*. A pelagic existence of shorter duration could explain the chunkier shape as opposed to the long, slender shape of pelagic juveniles of *P. maculatus*.

Figure 25.—Juvenile *Mullus auratus*. *Upper*. 47.2-mm. metamorphosed, trawled specimen (UMIM 3105). *Lower*. 45.8-mm. dip netted specimen. (BLBG)

TABLE 9.—*Relation of numbers of pectoral rays to standard length of 48 specimens of* Mullus auratus

[The upper number is the number of specimens, and the number in parentheses below is the approximate percentage for the respective size range]

Standard length (mm.)	Number of pectoral rays							Number of specimens
	11	12	13	14	15	16	17	
0–9.9	1 (50)	1 (50)						2
10.0–19.9		1 (12.5)	1 (12.5)		3 (37.5)	3 (37.5)		8
20.0–29.9					3 (42.9)	4 (57.1)		7
30.0–39.9					3 (60.0)	2 (40.0)		5
40.0–49.9					1 (25.0)	2 (50.0)	1 (25.0)	4
50.0–74.5						1 (100)		1
75.0–99.5						4 (100)		4
100.0–124.5						4 (80.0)	1 (20.0)	5
125.0–149.5					2 (28.6)	5 (71.4)		7
150.0–200.0						4 (80.0)	1 (20.0)	5

TABLE 10.—*Relation of total numbers of gill rakers to standard length of 48 specimens of* Mullus auratus

[The upper number is the number of specimens, and the number in parentheses below is the approximate percentage for the respective size range]

Standard length (mm.)	Total number of gill rakers								Number of specimens
	16	17	18	19	20	21	22	23	
0–9.9		1 (100)							1
10.0–19.9	1 (12.5)		1 (12.5)	3 (37.5)	1 (12.5)	2 (25.0)			8
20.0–29.9					4 (57.1)	2 (28.6)	1 (14.3)		7
30.0–39.9					1 (20.0)	2 (40.0)	2 (40.0)		5
40.0–49.9						3 (60.0)	1 (20.0)	1 (20.0)	5
50.0–74.9					1 (100)				1
75.0–99.9				3 (75.0)	1 (25.0)				4
100.0–124.5			1 (20.0)	3 (60.0)	1 (20.0)				5
125.0–149.5				4 (57.1)	2 (28.6)	1 (14.3)			7
150.0–200.0			2 (40.0)	1 (20.0)	1 (20.0)	1 (20.0)			5

TABLE 11.—*Relation of the numbers of lower-limb gill rakers (exclusive of one at angle of arch) to standard length of 48 specimens of* Mullus auratus

[The upper number is the number of specimens, and the number in parentheses below is the approximate percentage for the respective size range]

Standard length (mm.)	Number of lower-limb gill rakers						Number of specimens
	11	12	13	14	15	16	
0–9.9		1 (100)					1
10.0–19.9	1 (12.5)		3 (37.5)	4 (50.0)			8
20.0–29.9				5 (71.4)	2 (28.6)		7
30.0–39.9				3 (60.0)	2 (40.0)		5
40.0–49.9				1 (20.0)	3 (60.0)	1 (20.0)	5
50.0–74.9				1 (100)			1
75.0–99.9			2 (50.0)	2 (50.0)			4
100.0–124.5			3 (60.0)	2 (40.0)			5
125.0–149.5		1 (14.3)	1 (14.3)	5 (71.4)			7
150.0–200.0			3 (60.0)	1 (20.0)	1 (20.0)		5

TABLE 12.—*Collection and station data for 53 specimens of* Upeneus parvus examined

[Dip net (D), trawl (T), and stomach contents (SC)]

Station	Latitude	Longitude	Date of capture	Depth of water in which captured	Method of capture	Number of specimens and size range	Collection and catalogue number (if any)
				Fathoms		*mm.*	
WESTERN NORTH ATLANTIC: (Off North America)							
Silver Bay 1269	34°32′ N.	75°57′ W.	Sept. 12, 1959	25	T	(1) 106.0	BLBG
Silver Bay 1268	34°32′ N.	75°53′ W.	Sept. 11, 1959	30–31	T	(1) 105.0	BLBG
Combat 299	32°22′ N.	78°14′ W.	Apr. 21, 1957	250	D?	(1) 25.5	BLBG
GULF OF MEXICO:							
Oregon 1438	24°08′ N.	85°25′ W.	Jan. 29, 1956	2064	D	(1) 45.5	BLBG
Oregon 1313	28°05′ N.	88°46′ W.	June 9, 1955	980	D	(9) 22.0–32.0	CNHM 64714
Oregon 1145	28°17′ N.	87°52′ W.	July 26, 1954	1300	D	(1) 31.5	CNHM 64713
Oregon 1124	28°36′ N.	87°58′ W.	July 18, 1954	1200	D	(1) 25.5	TU 13073
Oregon 806	29°28′ N.	87°30′ W.	July 17, 1953	35	D?	(1) 34.0	TU 6869
Oregon 0.4, South of Dauphin Island; Mobile Bay, Ala.			Apr. 21, 1950			(1) 37.5	TU 13125
Oregon 1795	28°04′ N.	94°51′ W.	Mar. 16, 1957	35	T	(1) 64.5	CNHM 64232
Oregon 1100	27°00′ N.	93°55′ W.	June 11, 1954	600	D	(2) 28.5 and 143.0	TU 11739
Oregon 1102	26°58′ N.	91°55′ W.	June 12, 1954	600	D	(1) 28.0	TU 12838
Oregon 1035	26°10′ N.	92°00′ W.	May 8, 1954	890	D	(6) 46.5–60.5	CNHM 64712
Oregon 1089	26°10′ N.	96°25′ W.	June 4, 1954	10	D	(1) 50.0	BLBG
Oregon 1087	26°10′ N.	96°40′ W.	June 3, 1954	29	T	(3) 120.0–135.0	TU 10645
Oregon 1081	26°10′ N.	96°59′ W.	June 2, 1954	15	T	(4) 47.5–64.0	UF
Oregon 1078	26°05′ N.	95°25′ W.	May 27, 1954	1050	D	(1) 55.5	BLBG
Oregon 1038	25°30′ N.	92°00′ W.	May 10, 1954	1760	D	(1) 43.0	TU 10833
Oregon 1038	25°30′ N.	92°00′ W.	May 10, 1954	1760	D	(1) 50.0	BLBG
Oregon 1070	22°30′ N.	96°57′ W.	May 24, 1954	1056	D	(1) 23.5	TU 10885
Oregon 1485	22°20′ N.	97°05′ W.	Apr. 3, 1956	1060	D	(2) 21.0 and 21.5	TU 12789
Oregon 1057	18°45′ N.	93°15′ W.	May 16, 1954	19	T	(4) 113.5–128.5	USNM 158400
Oregon 1477	21°22′ N.	92°25′ W.	Mar. 29, 1956	114	D	(1) 26.5	UMIM
WESTERN NORTH ATLANTIC: (Off South America)							
Oregon 2221	09°22′ N.	59°13′ W.	Aug. 28, 1958	50	SC[1]	(1) 105.0	BLBG
Oregon 2274	06°54′ N.	55°40′ W.	Sept. 3, 1958	26–27	T	(2) 68.0 and 106.0	BLBG
Oregon 2304	06°12′ N.	52°34′ W.	Sept. 11, 1956	38	T	(1) 67.0	CNHM 64715
WESTERN SOUTH ATLANTIC:							
Vitoria, Brazil	20°18′ S.	40°20′ W.				(1) 172.4	SU 52245
Vitoria, Brazil	20°18′ S.	40°20′ W.				(1) 135.5	SU 52244
Entreposta da Pesca, Brazil						(1) 141.0	SU 52241

[1] Stomach contents from *Saurida normani* Longley.

GROWTH AND DEVELOPMENT

Juvenile *M. auratus* were easily distinguished from other young western North Atlantic Mullidae by the combined characters of a minute first dorsal spine and the characteristic tooth patch formed by the fusion of the vomerine and palatine bones (fig. 31). This patch was evident on all specimens over 14 mm. The absence of teeth in the upper jaw, a useful character in identification of the adults, is reevaluated under the section designated "teeth."

Larval *M. auratus*, 9.5–9.8 mm., are illustrated in figure 26. Except for incomplete ossification of the secondary caudal rays, the larvae had reached the juvenile stage.

At a size of 45.8 mm. (fig. 25, lower) the juveniles have acquired the barbels characteristic of the family, and the stripes on the first dorsal fin, characteristic of the adult, have appeared.

The transition from a pelagic to a bottom-living appearance (fig. 25, upper) takes place at approximately 47 mm. The pelagic juvenile coloration is lost, the adult coloration is acquired, and the body becomes more robust.

Figure 27 shows a 78.0-mm. specimen taken by bottom trawl, and at this size it had assumed the adult appearance.

Body Proportions

Thirteen of the body dimensions measured on a total of 49 specimens chosen at random except for size selection are plotted against standard length in figures 9 through 21.

The rate of increase in dimension of body part is constant throughout the size range of specimens examined for postorbital head length, snout to anal fin, body depth, snout to soft dorsal fin, ventral lobe of caudal fin, dorsal lobe of caudal fin, and interorbital space (figs. 10, 11, 12, 15, 16, 17, and 18, respectively). For barbel length, there is little if any change in dimension between 15 and 25 mm., after which there is an increase, and the rate of increase remains constant to the largest size (fig. 19). For head length and snout length an inflection occurs at about 45 mm., and the rate beyond this size is constant and slightly higher than below 45 mm. (figs. 9 and 20). For distance from snout to spinous dorsal fin, an inflection occurs at about 130 mm., with the rate of increase

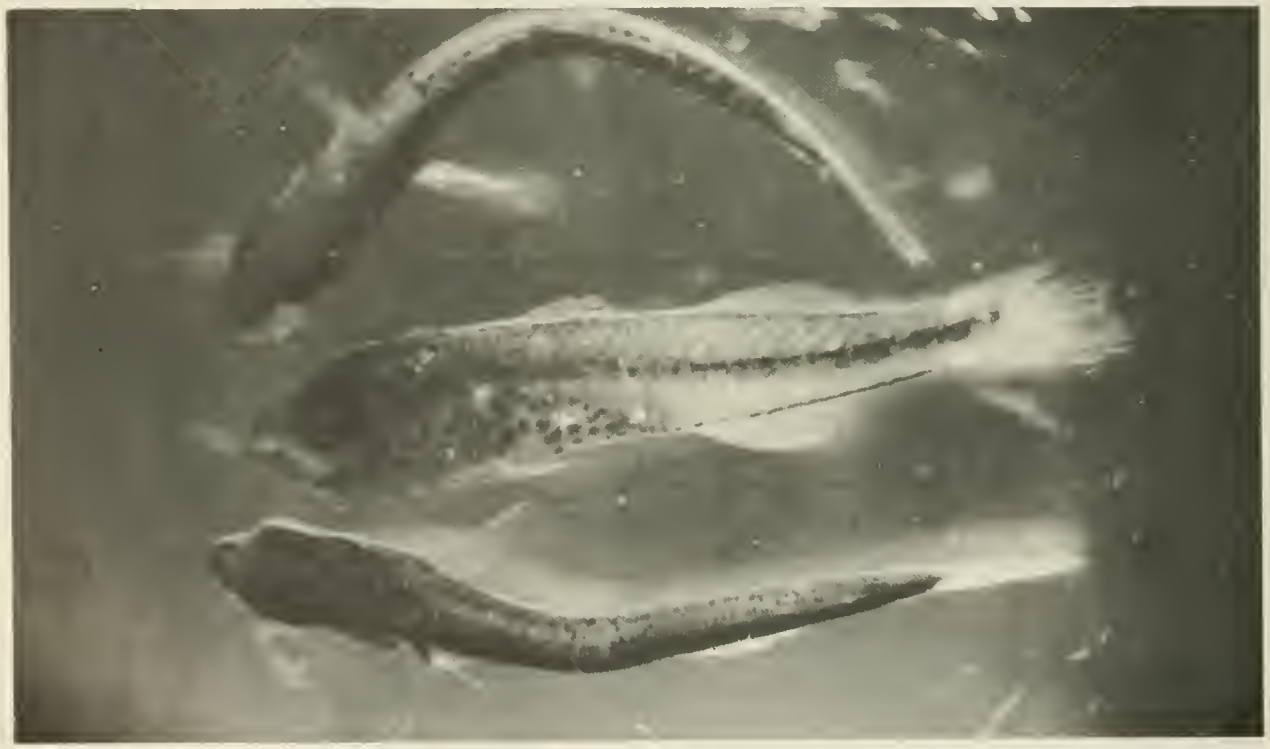

Figure 26.—Larval *Mullus auratus*. *Top:* 9.5 mm., ventral view; *middle:* 9.8 mm., lateral view; *bottom:* 9.6 mm., dorsal view. Dip netted by *Gill* personnel. (BLBG)

Figure 27.—78.0-mm. *Mullus auratus*. Trawled by *Oregon* personnel. (UF uncatalogued.)

beyond 130 mm. slightly higher than for smaller sizes (fig. 14). For length of first lower-limb gill raker the rate of increase beyond about 30 mm. is less than for sizes below 30 mm. (fig. 21); and for eye diameter the rate of increase beyond about 100 mm. is also slightly less than for smaller sizes (fig. 13).

There were too few 50- to 70-mm. *M. auratus* to demonstrate an abrupt increase in body depth at this size similar to that for *P. maculatus* (fig. 12). If *M. auratus* has this sudden increase in the body depth at the time of color metamorphosis (see Pigmentation., *M. auratus*), the graph could still show the same slope as it does. The increase could be apparent as a step rather than an upward inflection of slope, and this step would probably occur between 40 and 70 mm. as it does in metamorphosing *P. maculatus*. Even if this step does occur, juvenile *M. auratus* are not as slender-bodied as juvenile *P. maculatus*, and the step would probably not be as marked.

Pigmentation

The 9.5- and 33.6-mm. specimens discussed below were from the same dip net sample and were preserved in formalin. The photomicrograph (fig. 26) of larval *M. auratus* shows larvae 9.5 to 9.8 mm. in three views illustrating pigmentation. A lateral view (center larva) shows a series of horizontally elongated pigment patches along the lateral midline beginning at a point below the termination of the first dorsal fin and extending to the hypural bone. Above the lateral midline the surface was almost covered with light tan pigment which was without pattern. A line of darker pigment spots occurred adjacent to the second dorsal fin. Below the lateral midline, in the area between the posterior margin of the operculum and the origin of the anal fin, there were several large dark spots surrounded by buff-colored areas. The area above the anal fin was clear except for some pigment just below the lateral midline, and a row of dark chromatophores along the ventral midline.

In dorsal view (fig. 26, lowest specimen) there was a line of large pigment spots, dark in the center with tan radiations, on each side of the dorsal fins. These began behind the head and proceeded posteriorly as far as the secondary caudal rays. A long slender "V" was formed by the two rows as the body tapered toward the caudal fin. The cluster of pigment spots over the snout was marked when the specimen was viewed from this aspect.

The ventral view (uppermost in fig. 26) showed a similar "V," formed by a row of large pigment spots along each side on the ventral midline. Just posterior to the origin of the anal fin, the radiations from the dark centers of the chromatophores had so spread as to coalesce.

All of the fins were clear except the caudal which had a few scattered pigment spots on the base, giving the impression that they were mi-

grating posteriorly from the integument over the hypural bone.

A 17.5-mm. specimen showed light tan pigmentation diffused throughout the area that was clear in the 9-mm. specimens (that section below the lateral midline and above the anal fin). A few pigment spots were evident on both dorsal fins, and pigment had spread to about midway of the caudal fin.

In a 23.0-mm. specimen, pigmentation in the thoracic region appeared to be spreading from the large chromatophores seen in the smaller specimens. Just below the dorsal fins a second row of pigment spots was present above the row of chromatophores along the lateral midline. Anal, pelvic, and pectoral fins were still unpigmented. The chromatophores of the principal rays of the caudal fin had extended along the edges of the rays for about three-quarters their length.

In a 33.6-mm specimen, the pigmentation of the first dorsal fin had spread across the interspinous membranes to form a stripe about two-thirds of the distance from the base of the fin to the tips of the spines. The pigment spots about midway between this stripe and the base of the fin were grouped to indicate the formation of a second stripe. Other pigmentation remained the same.

In a 45.8-mm. formalin-preserved specimen (fig. 25, lower specimen), the second stripe of the first dorsal fin was complete across the interspinous membranes. In the distal one-third of the second dorsal fin there was a pigmented area on each ray just below a similarly pigmented area on the preceding ray. This gave the impression of a posteroventrally directed, oblique black stripe. A similar stripe, but extending through only the first four rays, was forming near the base of the fin.

The 47.2-mm. metamorphosed juvenile (fig. 25, upper specimen) had a uniform light tan background. The lower half of the body was clear of chromatophores except for tiny scattered pigment spots. The upper half retained some large pigment spots, and the scales had pigment on their margins. A third stripe had made its appearance on the second dorsal fin.

The 78.0-mm. specimen (fig. 27), preserved in isopropyl alcohol, was virtually devoid of scales and was tan throughout. There were no pigment spots in the body except for a few minute ones along the dorsal surface. This specimen was one of the few *M. auratus* I examined that retained pigmentation of the caudal fins. Pigment spots were grouped along the principal rays to form four bars in the upper lobe and five in the lower.

The following notes on the color of an adult *M. auratus* were taken from a specimen which had been in formalin for 13 days:

> Head red. Sides red above the lateral midline, shading to a silvery abdomen. Bright red stripe along midline, below which are two yellow stripes. Pectorals pink with four faint stripes (color not recorded). Pelvics clear with four yellow stripes. Anal yellow. First dorsal clear with two stripes, upper bright orange, lower yellow. Second dorsal clear with four stripes, yellow flecked with black. Dorsal half of caudal with seven or eight faint bars, some bright red, some orange, and some yellow. Ventral half of caudal with faint bars, the number indeterminate (color not recorded).

Specimens that had been in preservative for a considerable length of time were a pale yellow throughout and had lost all distinctive markings.

Fins

Spinous dorsal.—With one exception all of the specimens examined had eight spines in the first dorsal fin, including the small first spine (fig. 28). One specimen had seven spines including the small first spine.

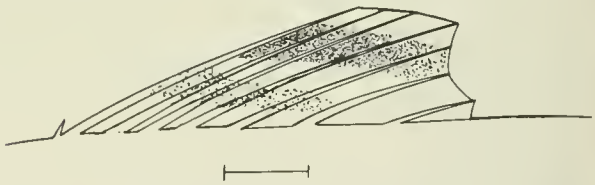

Figure 28.—Spinous dorsal fin of 44.9-mm. *Mullus auratus*. Line equals 2 mm.

Soft dorsal.—The adult complement is one unbranched ray plus eight branched rays.

At 11.9 mm. there was no segmentation, but the last eight rays were segmented on a 14.5-mm. specimen. The first ray did not usually segment before 47 mm.

The last ray was branched at 9 mm. Additional branching did not occur until 18 mm.; it was complete at 40 mm.

Pectoral.—All of the specimens examined showed an adult complement of 15 to 17 fin rays

after 16 mm. The numbers of fin rays are plotted against size in table 9, p. 434.

Segmentation began with the third ray at approximately 25 mm., then proceeded ventrally through the rays until the first ray and the last ray segmented at approximately 47 mm.

A 25-mm. specimen had no branched rays, but at 27 mm. there were four branched rays, the fourth through the seventh. At 47 mm. all except the first two rays were branched—the first two rays never branch.

Pelvic.—Segmentation apparently occurred simultaneously in all five soft rays. There was no segmentation in any of the specimens examined up to 14 mm., but specimens over 14.5 mm. had all pelvic soft rays segmented.

Branching, which had not occurred through 18.7 mm., was complete at 25 mm.

Anal.—All adult specimens examined had one spine, one unbranched ray, and six branched rays. Segmentation began at approximately 14 mm. and was complete by 16 mm.

The smallest specimen, 8.2 mm., had the last ray branched. Additional branching was not evident until 17 mm. and was complete at 21 mm.

Caudal.—There were 15 principal rays on all specimens examined. All principal rays were segmented at 9.3 mm.

The innermost rays were the first to branch, beginning at about 14 mm., and branching was complete on all specimens over 18.7 mm.

Between 14.5 and 42 mm. the number of secondary rays was 9 or 10 in the dorsal lobe and 8 to 10 in the ventral lobe. Nine is the usual number for each lobe. After 42 mm. the anterior rays were overgrown by tissue and scales and could not be counted.

At 9 mm. the five dorsal and four ventral secondary rays were unsegmented. On a stained 10.9-mm. specimen, there were eight unsegmented secondary rays in each lobe. At 14.5 mm. there were 18 secondary rays, and the first ray adjacent to the principal rays in both dorsal and ventral lobes had segmented. The secondary ray second from the principal caudal rays in each lobe was not segmented in fish less than about 45 mm. A cleared and stained 154.0-mm. adult had segmentation in only the first two secondaries adjacent to the principal rays in each lobe.

Gill rakers

Total and lower limb.—Both total number of gill rakers (16–23) and numbers of gill rakers on the lower limb (11–16, exclusive of the one at the angle of the arch) were counted on 48 specimens, ranging in size from 9 to 199 mm. Below 9 mm. counts were not reliable. Counts are plotted against size in tables 10 and 11, pp. 434, 435. In both instances there was an increase in average number of gill rakers with increase in size up to 50 mm., then the average number decreased with further increase in size of specimens (decrease was in the number of rudiments as they appeared to be overgrown by tissue).

Ceratobranchial bone.—Counted on 10 specimens (28.6 to 138.8 mm.), of which 1 had 9 gill rakers, 1 had 11, and the others had 10.

Teeth

Upper jaw.—Contrary to generic descriptions (based on adult specimens), *M. auratus* less than 50 mm. do have visible teeth in the upper jaw. Consequently, keys to the Mullidae which use the teeth to separate the genera are confusing when applied to specimens smaller than 50 mm., and the possibility exists that *M. auratus* may be involved.

The genus *Mullus* was first described by Linnaeus in the 10th edition of "Systema Naturae" (1758), but there was no mention of the teeth either in this or the 12th edition (1766). In the 13th edition (Linnaeus and Gmelin, 1789) the teeth were first mentioned (translation)—". . . mandibulae and palate armed with small teeth . . . ." Whether "mandibulae" refers to both upper and lower jaws, I can't say. Turton (1806) interpreted the word mandibulae as "jaws." Since Linnaeus, *Mullus* has been described in the literature as being without teeth in the upper jaw. Günther (1859) said of the teeth of the genus *Mullus*, ". . . none in upper jaw," and Jordan and Evermann (1896) used the same words, ". . . none in upper jaw . . . ." However, in the original description of *M. auratus* by Jordan and Gilbert (1882), which named *M. auratus* as a subspecies of *Mullus barbatus*, the authors stated, "Teeth . . . on upper jaw obsolete . . . ." Examination of the juveniles of the species has shown that this last observation by Jordan and Gilbert was accurate.

Small canine teeth were apparent on the upper jaw of *M. auratus* of 12 mm. A 21-mm. specimen had 3 or 4 teeth on each side of the upper jaw, and

a 37.0-mm. specimen (fig. 29) had about 15 teeth on each half of the premaxillary. These varied in size and pointed obliquely downward and toward the back of the mouth. They were freely movable in their sockets, but did not dislodge when teased with a probe. At 45 mm., many small teeth were evident, but the upper lip was beginning to overgrow and mask them. The upper lip continued this growth over the teeth, and in a 47-mm. specimen the lip had to be turned back to reveal the presence of three teeth on the left premaxillary bone and five on the right. No teeth were evident in larger specimens, even when the lip was turned back, but when the right premaxillary bone of a 106.5-mm. specimen was dissected and stained, two teeth were revealed (fig. 30). There were also two tooth sockets medial to the teeth. The premaxillary bone of a 154-mm. specimen was dissected and stained, but neither teeth nor tooth sockets were found.

Lower jaw.—No teeth were visible on the lower jaw of any specimen of *M. auratus* below 21 mm. A 37-mm. specimen had several small canine teeth in a single row toward the back of the mouth.

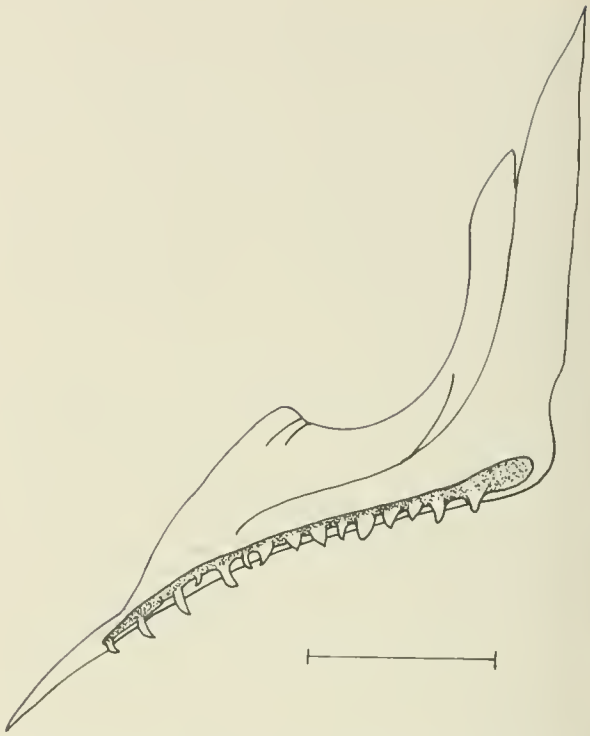

Figure 29.—Cleared and stained left premaxillary of 37.0-mm. *Mullus auratus*. Line equals 0.5 mm.

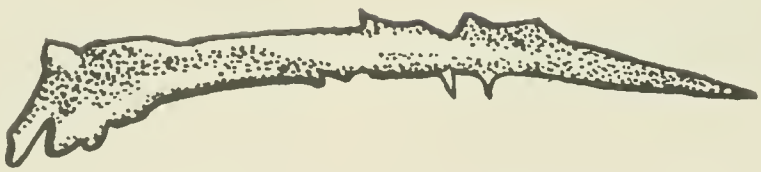

Figure 30.—Drawing of dissected and stained right premaxillary of 106.5-mm. *Mullus auratus*.

These teeth are irregularly biserial anteriorly—the adult arrangement of the small, inconspicuous teeth in the lower jaw.

Vomerine and palatine.—*M. auratus* has the characteristic tooth patch of the genus *Mullus*, formed by the joining of the vomer and palatine bones (Lachner, 1954). This character alone will serve to distinguish this species from the other western North Atlantic mulloid fishes.

At 10.9 mm. there was a single palato-vomerine bone patch on each side of the median line of the roof of the mouth, but no teeth were evident. A 17-mm. specimen had the bone patches, separated by 0.1 mm. at their closest point (the anterior ends), with three teeth on one patch and two on the other. A 37.0-mm. specimen had about 15 coarse, peglike, slightly pointed teeth present on each patch (fig. 31). These are similar to the tooth patches of the adult except for number of teeth. The stained and dissected palato-vomerine tooth patches of a 154-mm. specimen had about 55 teeth per patch.

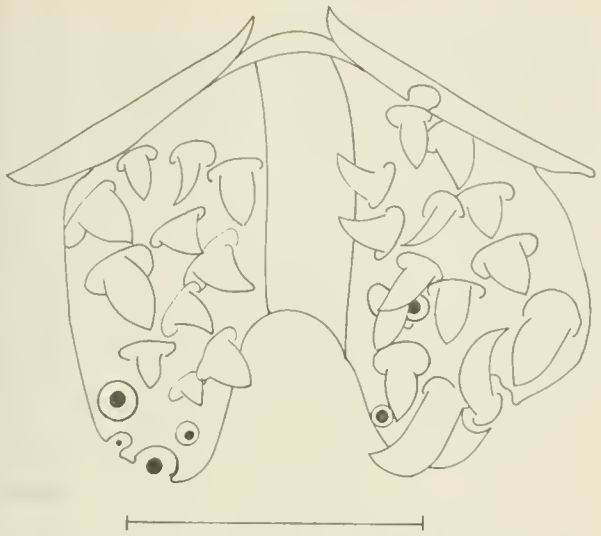

Figure 31.—Cleared and stained palato-vomerine tooth patch of 37.0-mm. *Mullus auratus*. Line equals 0.5 mm.

Scales

Lateral line scales were counted on 28 specimens ranging in size from 44.8 to 199.0 mm. The range in counts held for small sizes through the largest specimens, 29 to 35 (mean of 32), with 32 and 33 most frequently encountered. This is somewhat lower than the count of "about 40" given by Jordan and Evermann (1896) and Beebe and Tee-Van (1933) for *M. auratus*.

The extreme deciduousness of the scales during the pelagic stage is demonstrated by the following figures. One hundred and eight *M. auratus*, ranging in size from 9.3 to 36.4 mm., were examined in an attempt to determine the manner in which scale formation occurs. Fifty-one of these specimens, ranging from 9.3 to 34.4 mm., were totally devoid of scales. The 57 specimens with one or more scales ranged from 21.8 to 36.4 mm., and none had more than four scales in the lateral line. Scales present in the specimens below 30 mm. were usually around the dorsal fins and restricted to above the lateral line.

In a second series of 33 slightly larger specimens ranging from 19.6 to 45.8 mm., 12 specimens (19.6 to 37.4 mm.) had no scales. Two individuals, 44.8 and 45.3 mm., had 30 lateral line scales—these were the smallest specimens on which scale counts were possible.

A scale from a 25.5-mm. specimen lacked ctenii, but one from a 45-mm. specimen had about 10 ctenii. There were 65 ctenii on a scale from a 117-mm. specimen, and 186 on a scale from a 199-mm. adult.

Barbels

According to Lo Bianco (1907), Jobert (1872) was the first to advance the theory that the barbels of the family Mullidae are nothing more than displaced branchiostegal rays. Zincone (1876) had given the theory some consideration, but was forced to the conclusion that he could neither deny nor confirm the hypothesis, as the question could only be resolved embryologically, and he had been unable to obtain fertile eggs in aquaria. Lo Bianco (1907) quoted Raffaele (1888) as saying that, whereas he (Raffaele) was able to obtain the fertile eggs of *Mullus surmulletus*, which hatched in 3 to 4 days, the larvae died in 7 or 8 days after hatching, and there was no trace of tactile barbels at this stage of development. Lo Bianco said that he too had seen eggs laid in captivity by *Mullus*, and also effected artificial fertilization of both local species (*Mullus surmulletus* and *Mullus barbatus*), but the larvae died as soon as the yolk-sac was absorbed.

In the summer of 1906, Lo Bianco obtained a series of *Mullus* from the Gulf of Naples, 6 to 15 mm. in length, plus a few specimens 22, 26, and 30 mm. in length. From these he gave a detailed description of the development of the barbels, and in the summation of his work he stated (1907), "From this observation of mine is demonstrated the origin of the barbels of *Mullus from the first branchiostegal . . . .*"[4]

Also, Montalenti (1937) made this statement in regard to the Mullidae (translation), "In the pelagic individual about 35 mm. long the first branchiostegal ray detaches from the membrane and constitutes the barbels characteristic of this fish."

The series of *M. auratus* I examined demonstrated the barbels developed from the bone that appeared in the 8.2-mm. specimen to be the first branchiostegal ray. The barbel development is similar to that described by Lo Bianco for a Mediterranean *Mullus*, but occurs at a smaller size.

Figure 32 shows the position of the branchiostegals of an 8.2-mm. *M. auratus* which agreed in size and shape with those in Lo Bianco's illustration of an 8-mm. Mediterranean *Mullus* (1907, fig. 2). Lo Bianco's measurements were probably

[4] My translation of Lo Bianco's statement.

Figure 32.—Ventro-dorsal view of head of cleared and stained 8.2-mm. *Mullus auratus* showing position of branchiostegal rays. Line equals 1 mm.

expressed in total lengths. In the 8.2-mm. *M. auratus*, the position of the first ray was more anterior relative to the eyes and point of fusion of the branchiostegal membrane than in Lo Bianco's specimen; in these respects it conformed most closely with his illustration of a 22-mm. *Mullus* (Lo Bianco, 1907).

Two 19-mm. stained specimens of *M. auratus* showed the first branchiostegal rays displaced as far forward as the anterior edge of the eye. They still retained the same general shape as the other branchiostegal rays and were separated from each other by a distance of 0.3 mm. at their closest point. Barbel length was 2.3 mm. on one specimen and 2.6 mm. on the other. Three of the four barbels on the two specimens had detached from the branchiostegal membrane. Lo Bianco noted that this separation from the membrane occurred between 26 and 30 mm. in his series of *Mullus*. In *M. auratus*, one of the barbels was detached in a fish as small as 9 mm.; the barbel at this size measured less than 2 mm. One 14.5-mm. specimen had both barbels free. On the other hand, a 24.5-mm. specimen had one barbel still attached to the membrane. This is the largest specimen in which any barbel remained attached, and all of the specimens between 14.5 mm and 24.5 mm. had at least one barbel free.

At 28 mm. the bases of the barbels had shifted forward past the posterior edge of the mouth, and the anterior ends of the bases had joined together.

Operculum

The opercular bone (fig. 33) did not possess a spine on any specimen examined, and the posterior edge is rounded and smooth.

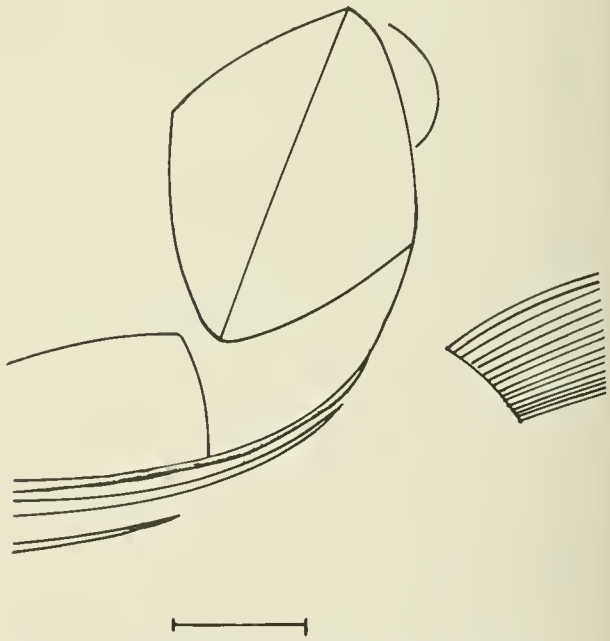

Figure 33.—Operculum and cleithrum of 44.9-mm. *Mullus auratus*. Line equals 2 mm.

Cleithrum

This small inconspicuous bone (fig. 33), almost covered by the opercular flap, had no serrations as it does in *P. maculatus*.

SPAWNING

The young *M. auratus* taken on the *Gill* cruises were all collected between January and May (table 7). The smallest specimen (8 mm.) was collected in April.

UPENEUS PARVUS POEY

DISTRIBUTION

Briggs (1958) gave the range of *Upeneus parvus* as eastern Florida to the Lesser Antilles and throughout the Gulf of Mexico. Lachner (1954) reported, "Known from . . . Cuba, Tobago (Norman, 1922), Puerto Rico, and Tortugas."

Several recent captures extend the range of *U. parvus* considerably northward. Two specimens were taken off Cape Lookout, N.C., by the U.S. Fish and Wildlife Service vessel *Silver Bay*, at successive stations, 1268 and 1269 (table 12), in depths of 25 to 30 fathoms. Also, included in the BLBG collection, there is a 26-mm. mullid, taken off the coast of South Carolina with 9 small *M. auratus*. It lacks the minute 1st dorsal spine and the palato-vomerine tooth patch typical of *M. auratus*. Its pigmentation and gill raker count of 5–1–17 (12 on the ceratobranchial bone) are typical of *U. parvus* at this size, and I have designated it as this species.

In addition, three specimens of this species were taken off the northeast coast of South America by the U.S. Fish and Wildlife Service vessel *Oregon* at stations 2221, 2274, and 2304 (table 12, p. 435), and I have examined three specimens from Brazil previously identified as *Pseudomulloides carmineus* Miranda-Ribeiro (Miranda-Ribeiro, 1915). Two were labeled "Vitoria, Brazil," and the third as simply "*Entraposta da Pesca*" (fish market?). The only differences I could find between these specimens and *U. parvus* were that they had one fewer lower-limb gill raker (17), and possibly a shorter barbel length and smaller eye. These differences, even if real, are not of specific or even subspecific importance. Ernest A. Lachner of the USNM, currently revising the Mullidae, identified them as *U. parvus*, which extends the southern range for this species to Vitoria, Brazil. The three specimens are included as *U. parvus* in table 12 and in these discussions. The labels from these Brazil specimens do not state that they were market-procured, but this could be the case. They could have been brought into the markets from some distance away, and the exact locality records may be questioned.

Figure 2 gives the locations of capture of the specimens examined; table 12 gives pertinent station data and present location of material.

ECOLOGY

Briggs reported (1958) that *U. parvus* is a shore fish, as are all of the four species of western North Atlantic Mullidae. This is supported by the data on specimens examined (table 12). All adult specimens over 100 mm. were taken by bottom trawls in water depths ranging from 19 to 50 fathoms (tables 13 and 14, p. 444). Longley and Hildebrand (1941) reported that this species was repeatedly taken in water depths of 40 to 60 fathoms. That they are bottom-dwellers is shown by their being taken consistently in bottom trawls.

The juveniles have an offshore pelagic stage that differs from the adult in appearance. The specimens examined on which complete station data are available ranged from 20.8 to 135.0 mm., and are individually listed in order of size in table 13. All specimens smaller than 47.5 mm. were taken by dip net. The locations of capture (table 12) show small specimens taken in the middle of the Gulf of Mexico (*Oregon* Stations 1035 and 1102). This is roughly 100 to 150 miles from the nearest shallow water, the Campeche Bank, and approximately 250 miles from the nearest major land mass (fig. 2). In this vicinity a branch of the Gulf Stream flows northwesterly from the Yucatan Channel toward Galveston, Texas (Leipper, 1954), so probably these fish were spawned in the shallow waters south of the Campeche Bank and carried across the 1,000-fathom line. All of the specimens over 60.7 mm. were taken by bottom trawl (table 13), indicating that, whereas metamorphosis can be delayed up to a point, juveniles over approximately 60 mm. either find their normal adult habitat and descend to the bottom, their normal adult habitat, or perish.

The dip-netted specimens, regardless of standard lengths, are long and slender, a shape typical of pelagic fish. They are dark brown, and in spite of preservation, some of them have retained the silvery abdomen common to a pelagic stage (Hubbs, 1941). None has lost the juvenile pigmentation. Except for one, which is discussed later, the shallow-water specimens from 47.5 to

TABLE 13.—*Collection and station data for 53 specimens of* Upeneus parvus, *by individual specimen by size*

[Dip net (D), trawl (T), and stomach contents (SC)]

Size	Station	Method of capture	Depth of water in which captured	Day and month of capture	Latitude	Longitude
mm.			*fathoms*			
20.8	*Oregon* 1485	D	1060	Apr. 3	22°20′ N.	97°05′ W.
21.6	*Oregon* 1485	D	1060	Apr. 3	22°20′ N.	97°05′ W.
22.2	*Oregon* 1313	D	980	June 9	28°05′ N.	88°46′ W.
23.3	*Oregon* 1070	D	1056	May 24	22°30′ N.	96°57′ W.
25.5	*Oregon* 1124	D	1200	July 18	28°36′ N.	87°58′ W.
25.7	*Combat* 299	D?	250	Apr. 21	32°22′ N.	78°14′ W.
26.7	*Oregon* 1477	D	114	Mar. 29	21°22′ N.	92°25′ W.
28.1	*Oregon* 1102	D	600	June 12	26°58′ N.	91°55′ W.
28.3	*Oregon* 1100	D	600	June 11	27°00′ N.	93°55′ W.
28.5	*Oregon* 1313	D	980	June 9	28°05′ N.	88°46′ W.
29.0	*Oregon* 1313	D	980	June 9	28°05′ N.	88°46′ W.
30.0	*Oregon* 1313	D	980	June 9	28°05′ N.	88°46′ W.
30.5	*Oregon* 1313	D	980	June 9	28°05′ N.	88°46′ W.
30.5	*Oregon* 1313	D	980	June 9	28°05′ N.	88°46′ W.
30.8	*Oregon* 1313	D	980	June 9	28°05′ N.	88°46′ W.
31.0	*Oregon* 1313	D	980	June 9	28°05′ N.	88°46′ W.
31.4	*Oregon* 1145	D	1300	July 26	28°17′ N.	87°52′ W.
32.1	*Oregon* 1313	D	980	June 9	28°05′ N.	88°46′ W.
34.0	*Oregon* 806	D?	35	July 17	29°28′ N.	87°30′ W.
37.5	*Oregon* 0.4	----------	----------	Apr. 21	South of Dauphin Island, Mobile Bay, Ala.	
43.0	*Oregon* 1038	D	1760	May 10	25°30′ N.	92°00′ W.
44.0	*Oregon* 1100	D	600	June 11	27°00′ N.	93°55′ W.
45.4	*Oregon* 1438	D?	2064	Jan. 29	24°08′ N.	85°25′ W.
46.5	*Oregon* 1035	D	890	May 8	26°40′ N.	92°00′ W.
47.5	*Oregon* 1081	T	15	June 2	26°10′ N.	96°59′ W.
50.0	*Oregon* 1089	D	40	June 4	26°10′ N.	96°25′ W.
50.5	*Oregon* 1038	D	1760	May 10	25°30′ N.	92°00′ W.
52.5	*Oregon* 1035	D	890	May 8	26°40′ N.	92°00′ W.
53.8	*Oregon* 1035	D	890	May 8	26°40′ N.	92°00′ W.
54.6	*Oregon* 1081	T	15	June 2	26°10′ N.	96°59′ W.
55.5	*Oregon* 1078	D	1050	May 27	26°05′ N.	95°25′ W.
56.6	*Oregon* 1035	D	890	May 8	26°40′ N.	92°00′ W.
58.0	*Oregon* 1035	D	890	May 8	26°40′ N.	92°00′ W.
59.5	*Oregon* 1081	T	15	June 2	26°10′ N.	96°59′ W.
60.7	*Oregon* 1035	D	890	May 8	26°40′ N.	92°00′ W.
64.2	*Oregon* 1081	T	15	June 2	26°10′ N.	96°59′ W.
64.5	*Oregon* 1795	T	35	Mar. 16	28°04′ N.	94°51′ W.
67.0	*Oregon* 2304	T	38	Sept. 11	06°12′ N.	52°34′ W.
67.9	*Oregon* 2274	T	27/26	Sept. 3	06°54′ N.	55°40′ W.
105.0	*Silver Bay* 1268	T	31/30	Sept. 11	34°32′ N.	75°53′ W.
[1] 105.0	*Oregon* 2221	SC	50	Aug. 28	09°22′ N.	59°43′ W.
106.0	*Oregon* 2274	T	27/26	Sept. 3	06°54′ N.	55°40′ W.
106.0	*Silver Bay* 1269	T	25	Sept. 12	34°32′ N.	75°57′ W.
113.5	*Oregon* 1057	T	19	May 16	18°45′ N.	93°15′ W.
116.5	*Oregon* 1057	T	19	May 16	18°45′ N.	93°15′ W.
120.0	*Oregon* 1087	T	29	June 3	26°10′ N.	96°40′ W.
127.0	*Oregon* 1057	T	19	May 16	18°45′ N.	93°15′ W.
128.5	*Oregon* 1057	T	19	May 16	18°45′ N.	93°15′ W.
129.5	*Oregon* 1087	T	29	June 3	26°10′ N.	96°40′ W.
135.0	*Oregon* 1087	T	29	June 3	26°10′ N.	96°40′ W.

[1] Stomach contents from *Saurida normani*.

TABLE 14.—*Relation of size of specimen, method of capture (dip net, D; trawl, T), and water depths in which captured for* Upeneus parvus

[Each letter represents a capture of one or more specimens within a particular size range]

DEPTH IN FATHOMS	SIZE RANGE IN MILLIMETERS				
	0–24.5	25.0–49.5	50.0–74.5	75.0–99.5	Over 100
Over 100	DDD	DDDD DDDD DD	DDD		
75–100					
50–74					
25–49		D	DTTT		TTTT
0–24		T	T		T

TABLE 15.—*Relation of the numbers of pectoral fin rays to standard length of 47 specimens of* Upeneus parvus

[The upper number is the number of specimens, and the number in parenthesis below is the approximate percentage for the respective size range]

Standard length (mm.)	Number of pectoral fin rays				Number of specimens
	13	14	15	16	
20.8–21.6	1 (50.0)	1 (50.0)			2
22.2–29.9		3 (33.3)	6 (66.7)		9
30.0–39.9		2 (25.0)	4 (50.0)	2 (25.0)	8
40.0–49.9		1 (20.0)	3 (60.0)	1 (20.0)	5
50.0–59.9		1 (11.1)	7 (77.8)	1 (11.1)	9
60.0–68.0		1 (20.0)	3 (60.0)	1 (20.0)	5
105.0–119.5			2 (40.0)	3 (60.0)	5
120.0–135.0			3 (75.0)	1 (25.0)	4

60.7 mm. taken by bottom trawl exhibit a completely different appearance from the dip-netted specimens of the same size taken usually over deep water. The metamorphosed specimens from shallow water are more robust. The changes that occur in dimensions of body parts between 40 and 60 mm. are reflected in the graphs of body proportions (figs. 9 through 21). A metamorphosed juvenile and a pelagic juvenile of similar size are shown in figure 34. The specimen uppermost in the photograph is 54.6 mm., taken at 15 fathoms by bottom trawl, and has the adult appearance. The lower specimen in the photograph is 52.5 mm., taken at the surface over deep water (890 fathoms) by dip net, and shows no evidence of metamorphosis.

A 67.9-mm. specimen taken by bottom trawl at a depth of 27 or 26 fathoms has the slender pelagic shape, but its coloration is intermediate between pelagic and bottom types. The juvenile pigmentation is still present on the snout and upper half of the body, but stripes are evident on the dorsal fins, and bars are present on the caudal fin (probably a metamorphosing form which has just reached its adult habitat).

GROWTH AND DEVELOPMENT

Young *U. parvus* below approximately 50 mm. had neither the vomerine nor the palatine teeth typical of the genus *Upeneus*.

Unlike *M. auratus* and *P. maculatus*, *U. parvus* had no visible minute first dorsal spine.

Gill raker counts (fig. 35) should serve to distinguish *U. parvus* from *M. martinicus* at sizes before the scales and teeth develop. No *M. martinicus* below 82.5 mm. have been examined, however, and the separation on gill raker counts is based on the assumption that the number of lower-limb gill rakers in *M. martinicus* prior to 82.5 mm. is not markedly smaller.

The smallest specimen examined, 20.8 mm., (fig. 36) was a juvenile. There were no major changes in the pelagic juvenile (fig. 34, lower) up to the time of transition, which occurred between 40 and 60 mm., after which the juvenile had the appearance of a young adult (fig. 34, upper).

Figure 34.—*Upper.* Bottom-living 54.6-mm. *Upeneus parvus* trawled by *Oregon* personnel. (UF) *Lower.* Pelagic 52.5-mm. *Upeneus parvus* dip netted by *Oregon* personnel. (CNHM 64712)

Body Proportions

Nine of the 13 body dimensions (measured on 53 specimens) plotted against standard length show an inflection in rate of increase with the initial rate lower than that beyond the point of inflection. For head length, body depth, eye diameter, snout to spinous dorsal fin, and snout to soft dorsal fin, the inflection occurs at about 60 to 70 mm. (figs. 9, 12, 13, 14, and 15, respectively); for snout to anal fin the inflection, at about 50 to 60 mm. (fig. 11); and for interorbital space, barbel length, and snout length, at about 40 to 50 mm. (figs. 18, 19, and 20, respectively). For length of first lower-limb gill raker an inflection occurs at about 40 to 50 mm., but the rate beyond about 50 mm. is lower than initially (fig. 21). Constant rates of increase throughout the size range of specimens examined are suggested for postorbital head length, and lengths of ventral and dorsal lobes of caudal fin (figs. 10, 16, and 17, respectively).

The inflections occur at or slightly after the time the juveniles move inshore to assume a bottom-dwelling existence.

Pigmentation

A 20.8-mm. specimen (fig. 36), preserved in isopropyl alcohol, had a medium tan background color. There was a lateral midline row of large dark pigment spots which extended from the upper posterior edge of the operculum to the

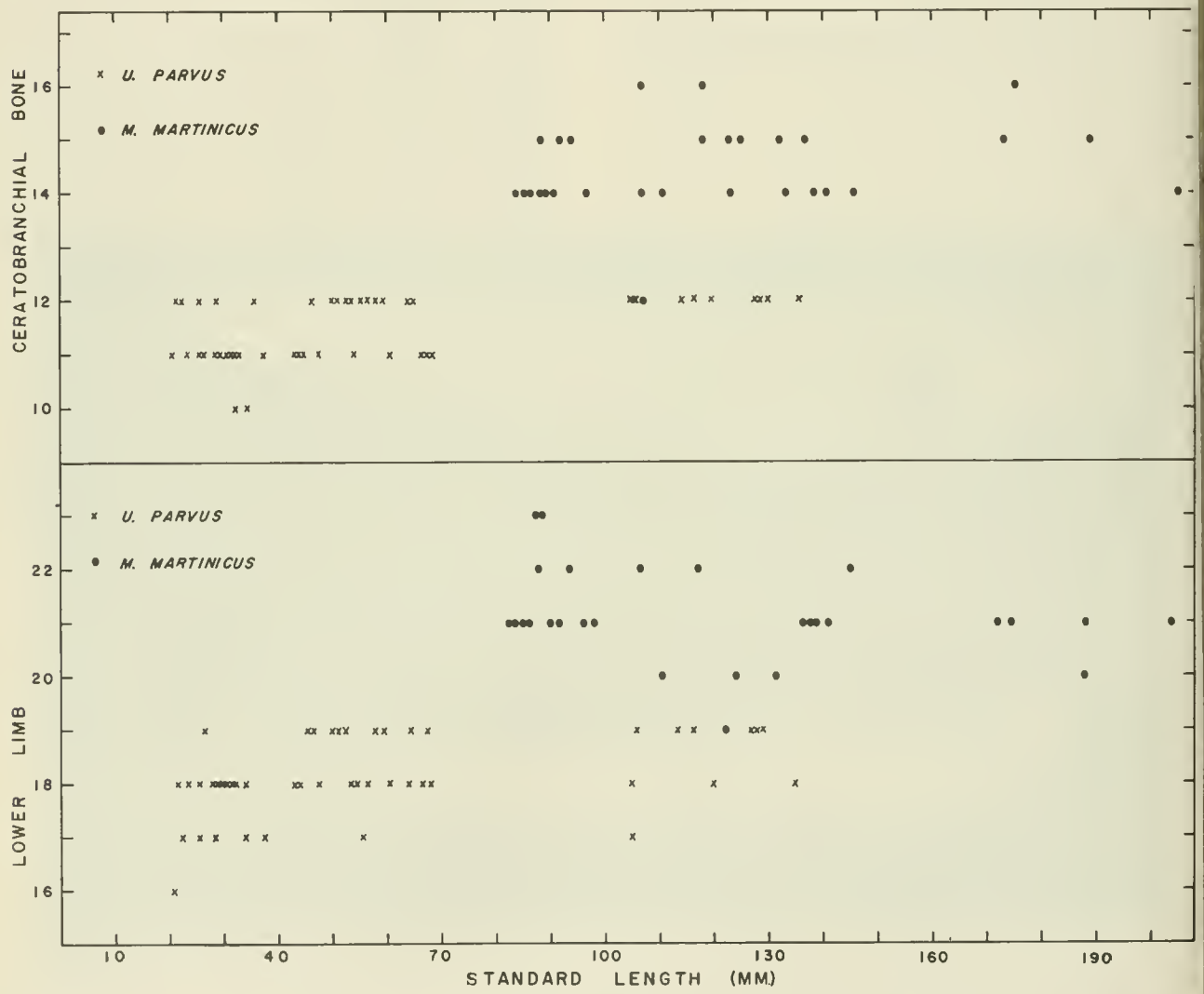

Figure 35.—Lower-limb and ceratobranchial-bone gill rakers of *Upeneus parvus* and *Mulloidichthys martinicus*.

Figure 36.—*Upeneus parvus*, 20.8-mm. Dipnetted by *Oregon* personnel. (TU 12789)
(Drawings 7, 30, and 36 by Mary Butler.)

hypural bone. Narrow strips immediately dorsal and ventral to the row were not pigmented, making the row of pigment spots particularly striking. About halfway between the lateral midline and the dorsal surface was a second row of lighter pigment spots also with unpigmented strips just dorsal and ventral which emphasized this row. Between the two rows the pigmentation consisted of scattered chromatophores. Above this second line of chromatophores, and beginning about midway between the two dorsal fins and extending to the insertion of the second dorsal, the pigment spots were arranged in short light bars which extended obliquely downward and posteriorly. Below the lateral midline, the pigment spots on the anterior half of the body were patternless, but, beginning about halfway between the operculum and the hypural base, they formed several oblique bars extending downward and posteriorly. The head was covered with a mingling of large and small chromatophores.

In dorsal view, a congregation of chromatophores was evident in the region of the snout. The dorsal surface of the body had a row of large pigment spots on each side of the dorsal fins, beginning just behind the head and extending to the secondary caudal rays. The two rows formed a long slender "V," as the body of the fish narrowed posteriorly.

A similar "V" was formed ventrally by a row of chromatophores on each side of the anal fin, beginning at the origin of the anal fin and extending to the secondary caudal rays. There were a few pigment spots on the rays of the first dorsal, the second dorsal, and the caudal fins. The pectoral, pelvic, and anal fins were clear.

The 52.5-mm. pelagic juvenile (fig. 34, lower specimen), preserved in alcohol, had a stripe of pigment spots along the lateral midline. This stripe was almost obscured on the anterior half of the body by heavy pigmentation, but was still prominent along the posterior half of the lateral midline. Above the midline, pigmentation was heavy and gave this section a dark brown color. Below the midline, the pigment spots, over a tan background, gradually became less dense and were very scattered on the ventral surface. Pigmentation on the head was dense, especially in the snout region. The fins had the same pigmentation as on the 20.8-mm. specimen, except for chromatophores over the rays of the dorsal half of the pectorals.

The 54.6-mm. metamorphosed shallow-water form (fig. 34, upper specimen) was preserved in isopropyl alcohol. The ground color was light tan with many pigment spots above the midline. Below the lateral midline, pigment spots were sparse. The pectoral, pelvic, and anal fins were clear. In the first dorsal, second dorsal, and anal fins, chromatophores were clustering to form the bars characteristic of the adult.

When Poey (1851) described *U. parvus*, he gave a color description. As the publication in which the description is found is not always available and, if available, the Spanish is old and difficult to translate, I include a translation of the color description here.

The back of the fish is bright red and it changes imperceptibly to white as it approaches the bottom of

the stomach. It has a yellow stripe running lengthwise down the side and others of the same color, but narrower, running below and parallel. It has yellow ventral and anal fins and the other fins are white with dark and narrow stripes . . . . The head does not bear yellow stripes; the dorsal and caudal fins have black stripes running obliquely from the front to the back; three in the first dorsal, two in the second, and five in each lobe of the tail, which is deeply indented . . . . I have seen some in May of 1852 of three, five, and six inches and none in the preceding years. Among those of three inches there was one which had five black spots under the yellow longitudinal stripes . . . .

The preserved specimens examined were pale yellow except for three or four black bars, invariably retained, on the ventral lobe of the caudal fin.

A mullid from the western North Atlantic that has retained these bars in preservative should be suspected of being *U. parvus*, as *M. auratus*, the other species that has bars on the caudal fin, (see Pigmentation, *Mullus auratus*) loses them very rapidly in preservative. *Mulloidichthys martinicus* is not reported as having a barred caudal (Longley and Hildebrand, 1941; Beebe and Tee-Van, 1928; Nichols, 1929), and I did not observe bars either. Nor were bars noted on the caudal fin of any of the 274 specimens of *P. maculatus* examined.

Fins

Spinous dorsal.—*U. parvus* had seven spines in the first dorsal (fig. 37). A minute first spine was lacking on all specimens.

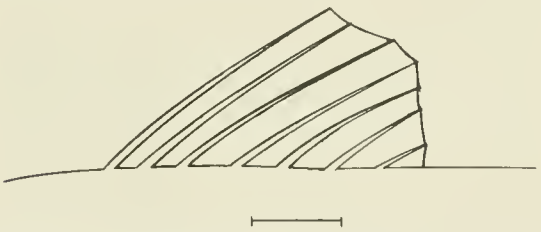

Figure 37.—Spinous dorsal fin of 44.0-mm. *Upeneus parvus*. Line equals 2 mm.

Soft dorsal.—The adults had a second dorsal ray count of one unbranched ray and eight branched rays, all segmented. The smallest specimen (20.8 mm.) had eight segmented rays, four of which were branched. The second ray, the last to branch in this fin, had branched at 43 mm.

The first ray, which was the last to segment, became segmented by about 26 mm.

Pectoral.—The number of pectoral rays in the larger specimens ranged from 14 to 16 (table 15, p. 444). Of the 23 specimens examined over 50 mm., 8.7 percent had 14, 65.2 percent had 15, and 26.1 percent had 16. Of the smaller specimens examined, only one had fewer than 14 rays, a 21.6-mm. specimen with 13 rays. The percentage of specimens with 15 or 16 rays, however, increases with size until a maximum is reached at some point between 68 and 105 mm., a range in which I had no specimens.

Segmentation was not manifest on either the 25.6- or 26.7-mm. specimens, but was on a 28.1-mm. specimen, and all rays were segmented by 60 mm. Segmentation proceeded in advance of branching, and the number of segmented rays exceeded the number of branched rays by two to four at all stages.

The first two rays were not branched on any specimen. Branching was complete on a 64.2-mm. specimen.

Pelvic.—The smallest specimen (20.8 mm.) had the adult complement of fin rays, I, 5, and the soft rays were all branched as well as segmented.

Anal.—The anal fin of the 20.8-mm. specimen has the adult complement of rays, I, i, 6. There were six segmented rays, four of which were branched. In a 21.6-mm. specimen segmentation was evident in all seven rays, and between 30 and 34 mm. branching was complete.

Caudal.—In the specimens examined the caudal fin principal ray count of the genus *Upeneus* was i, 7 + 6, i; this count agrees with that of Lachner (1954). A secondary ray counts on unstained or undissected material over 55 mm. were of dubious accuracy, but on 13 specimens up to this size I counted 16 secondary rays. On all specimens over 34 mm. the first two rays adjacent to the principal rays on both the dorsal and ventral lobes were segmented. Further segmentation of secondary rays was not studied, as no larger specimens were available for staining.

Gill rakers

Total number of gill rakers, number of lower-limb gill rakers, and number of gill rakers on the ceratobranchial bone were counted in specimens ranging in size from 20.8 to 172.5 mm. (tables 16 and 17, p. 449, and fig. 35).

TABLE 16.—*Relation of the total numbers of gill rakers to standard length of 54 specimens of* Upeneus parvus

[The upper number is the number of specimens, and the number in parentheses below is the approximate percentage for the respective size range]

Standard length (mm.)	Total number of gill rakers					Number of specimens
	23	24	25	26	27	
20.0–29.9	2 (18.2)	2 (18.2)	6 (54.5	1 (9.1)		11
30.0–39.9		3 (33.3)	5 (55.6)	1 (11.1)		9
40.0–49.9			2 (40.0)	2 (40.0)	1 (20.0)	5
50.0–74.9			5 (33.3)	4 (26.7)	6 (40.0)	15
75.0–99.9						--------
100.0–124.5			3 (37.5)	2 (25.0)	3 (37.5)	8
125.0–149.5		1 (20.0)	1 (20.0)	1 (20.0)	2 (40.0)	5
150.0–200.0				1 (100)		1

TABLE 17.—*Relation of the numbers of lower-limb gill rakers (exclusive of one at angle of arch) to standard length of 54 specimens of* Upeneus parvus

[The upper number is the number of specimens, and the number in parentheses below is the approximate percentage for the respective size range]

Standard length (mm.)	Number of lower-limb gill rakers				Number of specimens
	16	17	18	19	
20.0–29.9	1 (9.1)	3 (27.3)	6 (54.5)	1 (9.1)	11
30.0–39.9		2 (22.2)	7 (77.8)		9
40.0–49.9			3 (60.0)	2 (40.0)	5
50.0–74.9		1 (6.7)	7 (46.7)	7 (46.7)	15
75.0–99.9					—
100.0–124.5		2 (25.0)	2 (25.0)	4 (50.0)	8
125.0–149.5		1 (20.0)	1 (20.0)	3 (60.0)	5
150.0–200.0		1 (100)			1

TABLE 18.—*Collection and station data for 35 specimens of* Mulloidichthys martinicus *examined*

[Market procured (M), trawl (T), and collected with rotenone (R)]

Station	Latitude	Longitude	Date of capture	Depth of water in which captured	Method of capture	Number of specimens and size range	Collection and catalogue number (if any)
WESTERN NORTH ATLANTIC:				*Fathoms*		*mm.*	
5 mi. west of Nassau, Bahamas	[1]25°05′ N.	77°30′ W.	Aug. 11, 1958	0–1	R	(2) 85.0 and 90.0	UF
Nassau Fish Market, Bahamas			Aug. 17–20, 1955		M	(2) 172.5 and 204	UF 3534
Clifton Pier, New Providence Island, Bahamas.	[1]25°02′ N.	77°35′ W.	Aug. 11, 1958	1–2	R	(5) 83.5–106.5	UF
Key West, Fla						(1) 145.0	SU 508
GULF OF MEXICO:							
Oregon Campeche Banks			Dec. 7, 1952			(2) 98.0 and 145.0	CNHM 59818
CARIBBEAN SEA:							
Havana, Cuba						(1) 205.0	CAS IUM 26913
Havana, Cuba						(1) 137.5	SU 1724
Havana, Cuba						(1) 146.5	CAS IUM 2670
Kingston Market, Jamaica			Apr. 24, 1959		M	(5) 122.5–140.5	DKC.
Kingston Market, Jamaica			June 1957		M	(1) 188.0	DKC.
St. Croix, West Indies						(3) 85.5–110.0	CAS IUM 12375.
St. Croix, West Indies						(1) 82.5	SU 21854.
British West Indies						(4) 217.5–246.0	SU 4768.
Oregon 2625	18°45′ N.	64°46′ W.	Sept. 28, 1959	38	T	(1) 174.5	BLBG.
WESTERN SOUTH ATLANTIC:							
Recife, Brazil	08°03′ S.	34°51′ W.				(2) 117.5 and 131.5	SU 52250.
Salvador, Brazil	13°00′ S.	38°31′ W.				(2) 88.0 and 91.5	SU 52242.
Salvador, Brazil	13°00′ S.	38°31′ W.				(1) 94.0	SU 52243.

[1] Approximate latitude and longitude.

Total.—The adult complement of total number of gill rakers (25–27) was reached by 40 mm. (table 16, p. 449).

Lower limb.—The adult complement (17–19) also was attained by 40 mm., but the percentage of specimens with 19 continued to increase through 150.00 mm. (table 17, p. 449).

Ceratobranchial bone and comparison with M. martinicus.—The data indicate that the juveniles of *U. parvus* and *M. martinicus* may be separated on gill raker counts. The gill rakers of *U. parvus* are plotted against those of *M. martinicus* to show both the number of gill rakers on the lower limb and the number of gill rakers on the ceratobranchial bone (fig. 35). The latter character shows less intraspecific variation than the former. The terminus of the ceratobranchial bone was determined by manipulation of the gill arch and observation of the point that the break occurs between the ceratobranchial and basibranchial bones. The gill raker that may seem to occur between the two bones is included in counts for the ceratobranchial bone.

The graphs show a clear separation of the species *U. parvus* and *M. martinicus*. Up to a size of 34 mm., *U. parvus* possessed 10 to 12 gill rakers on the ceratobranchial bone, and 11 or 12 after this size. Above 82 mm., *M. martinicus* had 14 to 15, except for a 107-mm. specimen with 12 gill rakers on the right side (the side normally counted) but 14 on the left. The maximum number of lower-limb gill rakers in *U. parvus* was 19, and the minimum in *M. martinicus* was usually 20 or more (one specimen of *M. martinicus* had 19).

Teeth

Upper jaw.—Teeth were present in the upper jaw of all the specimens examined; the smallest was 20.8 mm.

Lower jaw.—No teeth were evident in the lower jaw of the 20.8- or 21.6-mm. specimens and one 28.0-mm. specimen, but were seen in all others.

Vomerine.—No teeth were apparent on the vomerine bone in a stained specimen of 44.0 mm., but they had formed in the 45.6-mm. specimen. Small teeth were present in all juveniles larger than 44 mm., with the exception of one 52.5-mm. specimen.

Palatine.—The palatine teeth seemed more variable than the vomerine in the time of their formation. They were present in a 45.4-mm. juvenile and in all of the specimens over 53.8 mm., but in the interval between these sizes some of the specimens had them and some did not. In the more mature forms, the number of palatine teeth increased rapidly, and the palatine bones of the adults presented coarse, slightly pointed, peglike teeth which were very much more numerous than the vomerine teeth.

Scales

Counts were possible on only a few specimens as the scales are very deciduous. A 22.0-mm. specimen, however, had 37 fully developed ctenoid scales in the lateral line, which is within the adult complement (36 to 38) (Lachner, 1954).

A 56-mm. specimen had 10 ctenii on the margin of one of the scales, and there were 55 on a scale of a 129.5-mm. specimen.

Barbels

In the smallest specimen, 20.8 mm., the right barbel was completely free of the branchiostegal membrane, but the left had not yet separated. The 21.6-mm. specimen had both barbels still attached. The 22.2-mm. specimen had the left barbel attached completely and the right barbel almost free, but still attached at the distal end. The 23.3-mm. and larger specimens had perfectly formed barbels free of the membrane. Thus, in *U. parvus* we have somewhat earlier development of the barbels than in *M. barbatus* or *M. surmulletus* as described by Lo Bianco (1907).

Operculum

No opercular spine was present on any specimen examined, although there was a projection of the opercular bone (fig. 38) in the same location as the opercular spine of *P. maculatus* and *M. martinicus* (figs. 23 and 43).

Cleithrum

When the scales were removed the cleithrum (fig. 38) was revealed as a prominent bone without the serrations found on the upper wing of the cleithrum of *P. maculatus* (fig. 23).

SPAWNING

The gonads of mature specimens, one male, 120 mm., and two females, 130 and 135 mm., taken by bottom trawl at 29 fathoms, June 3, 1954, in the Gulf of Mexico were found to be between stages IV and V in their development (the eggs or milt fill from one-half to the entire body cavity) using the classification given by Broadhead (1953).

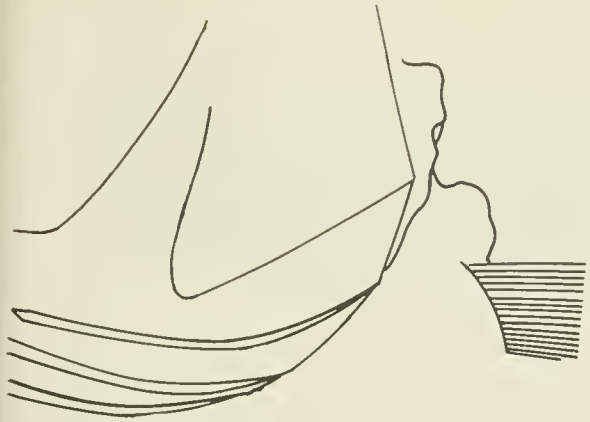

Figure 38.—Operculum and cleithrum of 44.0-mm. *Upeneus parvus*. Line equals 2 mm.

MULLOIDICHTHYS MARTINICUS (CUVIER)

No juveniles below 82.5 mm. were available for examination. Neither the exploratory operations of the *Theodore N. Gill* off the south Atlantic coast of the United States, nor the extensive work done by the *Oregon* in the Gulf of Mexico and in the Caribbean resulted in the capture of any specimen of this species below 82.5 mm. Other likely sources of material were investigated without success.

The likelihood of the appearance of these juveniles in the waters off the south Atlantic coast of the United States necessitates the inclusion of this species in a study of juvenile Mullidae of these waters, and they are discussed within the limits of the material available. Pertinent station data and present location of the material examined are listed in table 18, p. 449.

DISTRIBUTION

Briggs (1958) listed the range of *Mulloidichthys martinicus* as Bermuda and the Florida Keys to the Lesser Antilles, Panama, and the western Gulf of Mexico.

I examined adult specimens of this species from as far south as Salvador, Brazil, but as these could have been market-procured (data not given), the precise locality of their capture may be questioned. Locations of captures of the material examined are shown in figure 24.

ECOLOGY

An enigma is posed by the absence of juveniles of *M. martinicus* in collections where they might be anticipated. Parr (1930) noted this absence of pelagic specimens of *M. martinicus* in his collecting in the Bahamas and Turks Island (surface light at night) where the adults are plentiful, and referred to it as "peculiar." My smallest specimen with data (83.5 mm., table 18) was taken with aid of rotenone in 6 to 8 feet of water. The data on much of the material were scanty, but one large specimen was taken by bottom trawl.

GROWTH AND DEVELOPMENT

The smallest *M. martinicus* examined was 82.5 mm. (fig. 39). At this size, there was no external evidence of a minute first dorsal spine, a strong opercular spine was evident, and the anterior teeth in both upper and lower jaws were irregularly biserial.

Figure 39.—*Mulloidichthys martinicus*, 82.5 mm. (SU 21854)

Body Proportions

Thirteen body proportions were measured on 27 specimens from 82.5 to 204.0 mm. (figs. 9 through 21).

There is possibly a slight inflection between 150 and 180 mm. for interorbital space (fig. 18), with a suggestion of a lower rate of increase beyond the inflection than initially. The other characters show a constant rate of increase within the size range of available material.

Pigmentation

Specimens up to 122 mm. that were preserved in alcohol were either pale yellow overall or yellow with silvery abdomen and sides up to the lateral midline. Above this size, the colors were dark to light tan or yellow. Some retained red on the head and anteriorly on the lateral midline. Two, 174.5 and 188.0 mm., were tan with dark lateral midlines. Fins were clear on all specimens.

Fins

Spinous dorsal.—The literature is conflicting in regard to the number of spines. Opinion is about equally divided as to whether there are 7 spines (Cuvier and Valenciennes, 1829; Storer, 1846; Meek and Hildebrand, 1923; Beebe and Tee-Van, 1933) or 8 (Jordan and Evermann, 1896; Nichols, 1929; Evermann and Marsh, 1902). An examination of 27 specimens of the species explains the divergence of opinion. Visual examination shows some have a spiny protuberance resembling a very short spine at the origin of the 1st dorsal. If the area is carefully probed, some specimens show this structure embedded and on others probing reveals nothing (fig. 40). When present, the spiny protuberance is usually movable in all directions. A cleared and stained spinous dorsal fin of a 138.5-mm. specimen (fig. 41) shows the structure, completely covered by soft tissue.

I X-rayed similar-sized specimens of the four species of western North Atlantic Mullidae to observe the bony structure anterior to the spinous dorsal, seen on some, but not all, species (fig. 42). X–ray evidence points to an intergrading of this character between species. The species are arranged from top to bottom in the X-ray positive in ascending order of magnitude of the bony structure.

In *U. parvus* (106.0 mm.) the spiny protuberance at the origin of the first dorsal fin was small, round and well covered with soft tissue. The

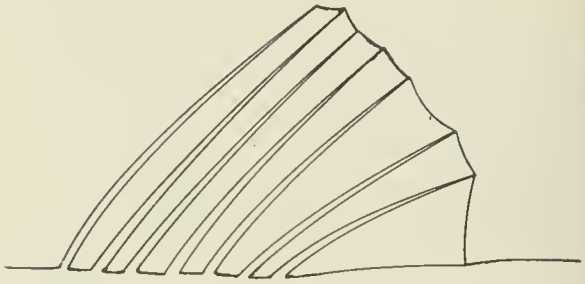

Figure 40.—Spinous dorsal fin of 83.5-mm. *Mulloidichthys martinicus*. Line equals 5 mm.

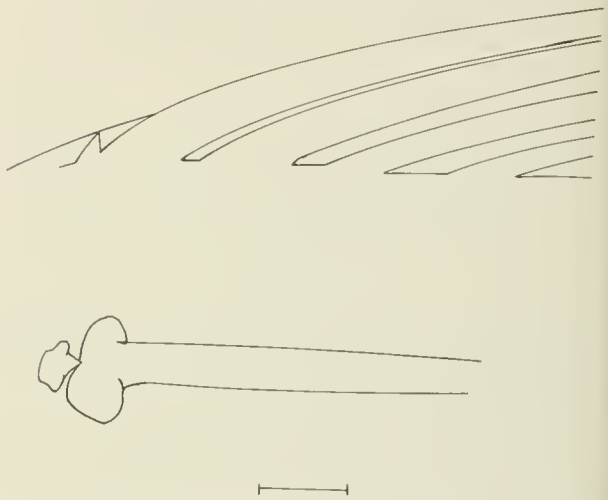

Figure 41.—Cleared and stained spinous dorsal fin of 138.5-mm. *Mulloidichthys martinicus*. *Upper:* lateral view; *lower:* dorso-ventral view. Line equals 2 mm.

interneurals numbered three and were set well in advance of the spines.

In *M. martinicus* (105.5 mm.) the structure was small, pointed obliquely up and back, and was covered with soft tissue. The interneurals numbered three (first not dense), and were set well in advance of the spines.

In *M. auratus* (105.5 mm.) the structure gave the appearance of a rudimentary spine. The interneurals numbered three and were not placed as far forward as in the two previously mentioned species. The spine protruded from the soft tissue.

In *P. maculatus* (106.5 mm.) the structure gave the appearance of a rudimentary spine, slightly larger than that of *M. auratus*. It projected well beyond the soft tissue. What appeared in the

Figure 42.—X-ray positive of Mullidae of the western North Atlantic. In descending order: 106.0-mm. *Upeneus parvus*, 105.5-mm. *Mulloidichthys martinicus*, 105.5-mm. *Mullus auratus*, and 106.5-mm. *Pseudupeneus maculatus*.

X-ray to be the third interneural was located farther posteriorly than in the other species and appeared to articulate with the rudimentary spine. All species appear to have seven pterygiophores, although there may be a question in *P. maculatus* as to whether the bone with which the minute spine articulates is properly termed an interneural or a pterygiophore.

Soft dorsal.—On all material there were nine segmented soft rays, eight of which were branched.

Pectoral.—Counts on 27 specimens ranged from 15 (twice) to 17 (once). In an 83.5-mm. specimen the first and the last two rays were not segmented. The first ray was the last to segment; it was segmented in a 140.3-mm. specimen. In the 83.5-mm. specimen, the first two and the last two rays were not branched, but the last two rays were branched at approximately 138 mm. The first two rays never branched.

Pelvic.—Rays numbered I, 5—all five soft rays branched and segmented by 82.5 mm.

Anal.—Rays numbered I, i, 6 on all material.

Caudal.—Principal rays numbered i, 7+6, i on 10 specimens. The secondary rays were overgrown with tissue in all material. None of the material was stained. It was not possible to count the number of secondary rays, even in the X-ray specimens (fig. 42).

Gill Rakers

Total.—Total numbers of gill rakers of 25 specimens were correlated with size ranges (table 19, p. 449). They ranged from 26 to 33 with 26, 27, and 33 encountered only once each. The larger specimens averaged fewer gill rakers as the rudiments become overgrown with tissue.

Lower limb and ceratobranchial bone.—The lower-limb gill rakers and those of the ceratobranchial bone are discussed and compared with those of *U. parvus* in the section on *U. parvus* (fig. 35).

The material from the more southern latitudes tended to have higher numbers of gill rakers on the ceratobranchial bone; 2 of the 3 specimens with 16 are from Brazil and the other from St. Croix.

TABLE 19.—*Relation of total numbers of gill rakers to standard length of 25 specimens of* Mulloidichthys martinicus

[The upper number is the number of specimens, and the number in parentheses below is the approximate percentage for the respective size range]

Standard length (mm.)	Total number of gill rakers								Number of specimens
	26	27	28	29	30	31	32	33	
82.5–99.5			1 (10.0)	2 (20.0)	3 (30.0)	1 (10.0)	2 (20.0)	1 (10.0)	10
100.0–124.5		1 (16.7)	1 (16.7)	2 (33.3)		1 (16.7)	1 (16.7)		6
125.0–149.5				2 (40.0)	2 (40.0)	1 (20.0)			5
150.0–204.0	1 (25.0)		1 (25.0)	1 (25.0)	1 (25.0)				4

Teeth

Upper and lower jaw.—All specimens had a row of small canines posteriorly in each jaw; these rows were irregularly biserial anteriorly.

Vomerine and palatine.—Absent.

Scales

Counts ranged from 34 to 39 (mean of 36) on 21 specimens, with 35 being the number most frequently encountered. The scale of a 138.0-mm. specimen had 83 etenii, and one from a 188.0-mm. specimen had 122.

Barbels

Fully developed and normal on all material.

Operculum

All material had a strong spine on the operculum at the anterior terminus of the lateral midline. Slightly dorsal to this is a small crenulated tab (fig. 43).

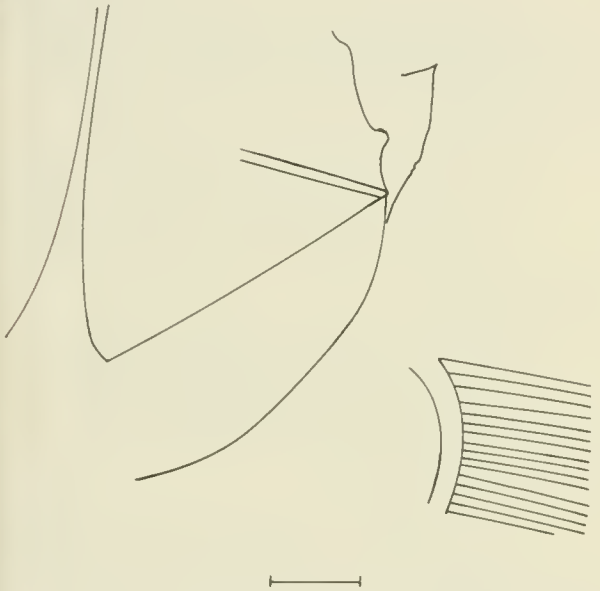

Figure 43.—Operculum and cleithrum of 83.5-mm. *Mulloidichthys martinicus*. Line equals 2 mm.

Cleithrum

No serrations were observed on the posterior wing of the cleithrum of any specimen.

ACKNOWLEDGMENTS

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FOOD OF ALBACORE TUNA, *THUNNUS GERMO* (LACÉPÈDE), IN THE CENTRAL AND NORTHEASTERN PACIFIC

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Bureau of Commercial Fisheries

The food study described in this report was undertaken at the United States Bureau of Commercial Fisheries Biological Laboratory, Honolulu,[1] as part of research studies on the highseas fishery resources of the tropical, subtropical, and temperate central Pacific. These studies have centered mainly on tunas since, as a source of human food, they are the most widely exploited pelagic species in this area.

Investigations on the food and feeding habits of tunas were initiated because other studies have indicated that the availability of food is an important factor in the abundance and distribution of some fish (Hardy, Lucas, Henderson, and Fraser, 1936; Hansen, 1949).

Albacore are widely distributed throughout the tropical, subtropical, and temperate waters of the Pacific. In temperate waters they are taken by surface trolling, pole-and-line, gill netting, and by longline fishing (Graham, 1957; Suda, 1954), while in tropical waters they are found only subsurface and are captured by longlining (Murphy and Shomura, 1953). Results of tagging experiments have shown that albacore are capable of extensive migrations. For example, two fish tagged off the west coast of North America were retaken in the vicinity of Japan; the distances traveled were 4,230 and 4,300 miles respectively. Such tagging results suggest that one population of albacore in the North Pacific may be supporting three fisheries (Otsu, 1960). In the temperate North Pacific albacore are fished by the Japanese in the west mainly during the spring and summer, in midocean in the winter, and by North Americans off the west coast during summer and fall. Japanese also take albacore in a longline fishery in the central and western Pacific from equatorial waters to about latitude 30° S.

The purposes of this study were:

1. To describe the food of albacore tuna caught in the central and northeastern Pacific.
2. To determine whether the abundance and distribution of albacore are related to the abundance and distribution of their food.
3. To determine whether feeding is related to such variables as method of capture of the albacore, their size, geographic location, season, and environmental factors.

There are numerous accounts in the literature of the food of albacore. Although reports for Pacific albacore outnumber those (principally by French workers) for the North Atlantic, most are fragmentary.

One of the earliest notes on the Pacific stocks (Bennett, 1840) described albacore as "voracious and miscellaneous feeders," and reported flying fish, "calmars," and small schooling fish as their natural food. Bennett listed the following as having been found in albacore stomachs: "Ostracions," filefish, sucking fish, "janthina shells," pelagic crabs, bonita, dolphin, and paper nautilus. Phyllosomas, larval sunfish, and part of a bigeye tuna had been eaten by albacore taken near the Bonin Islands (Kishinouye, 1917). The Japanese Bureau of Fisheries (1939, 1940) reported albacore food as sardine, saury, pomfret, squid, octopus, isopods, mysids, euphausiids, and heteropods. Kanamura and Yazaki (1940) found squid, octopus, stomatopods, barracuda, "hairtail," "flathead," "ginkagami" (*Mene maculata*), and "sardine" (*Bathylagus nakazawai*) in the stomachs of albacore from the South China Sea. Hart, et al. (1948) have presented a summary of albacore stomach contents sampled off Vancouver Island and the coast of Washington from 1941 to 1947. Saury, anchovy, lantern fish, pilchard, "red feed" (i.e., euphausiids), and squid were frequently occurring food items. Powell (1950) recorded small rockcod as an important food of albacore taken in the northeastern Pacific, with squid, saury, blackcod, and myetophids also present.

[1] Formerly the Pacific Oceanic Fishery Investigations (POFI).

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In a food study of 321 albacore troll-caught off California and Baja California, McHugh (1952) reported each of these 11 food items occurring in more than 10 percent of the stomachs: squid, saury (*Cololabis saira*), euphausiids, amphipods, the decapod crustacean *Pleuroncodes planipes*, paralepidids, rockfish (*Sebastodes* sp.), the gonostomatid *Vinciguerria lucetia*, hake (*Merluccius productus*), myctophids, and the anchovy *Engraulis mordax mordax*. The bulk of the food, however, was composed of saury (50 percent), squid (12 percent), and *P. planipes* (11 percent). Yabuta (1953) found barracuda, the trunkfish *Ostracion diaphanus* (=*Lactoria diaphanus*), and a species of "sand borer" in the food of albacore from seas adjacent to the Bonin Islands. He states, however, that "their feed are mostly crustacea and very small cephalopoda; therefore it is considered to have strong characteristics of a plankton feeder."

Koga (1958a, 1958b) described the food of albacore from the western Indian Ocean and the equatorial South Pacific. Twelve fish families occurred in the stomach contents of the western Indian Ocean albacore, with Plagyodontidae (=*Alepisauridae*), Triacanthidae, Carangidae, and Acinaceidae (=*Gempylidae*) found in 10 percent or more of the stomachs. Among the Crustacea, isopods, decapods, and stomatopods occurred in 10 percent or more of the stomachs. Squid occurred in 67 percent. Koga also found 12 fish families represented in the food of equatorial South Pacific albacore, with the following present in the food by 10 percent or more: Plagyodontidae, Triacanthidae, Acinaceidae, Ostraciidae, and Menidae. Decapod crustaceans occurred in 15 percent, squid in 50 percent, and octopods in 10 percent of the fish.

In the eastern North Atlantic albacore food was studied by Collett (1896), who reported finding these nine categories of fish in albacore taken in the Gulf of Gascony: horse mackerel (*Trachurus trachurus*), boarfish (*Capros aper*), barracudina (*Paralepis pseudocoregonoides*), lancet fish (*Plagyodus* sp.), *Scomberesox saurus* (the Atlantic counterpart of the Pacific saury), hatchet fish (*Sternoptyx diaphana*), gonostomatids (*Maurolicus* sp.), and pipefish (*Syngnathus aequoreus*). Joubin and Roule (1918) found *S. saurus*, the amphipod *Euthemisto bispinosa*, and *Paralepis* sp. to be the most important items of the diet of albacore caught off the coasts of Brittany, but also found the hatchet fish, *Argyropelecus olfersi*, a hoplophorid crustacean of the genus *Acanthephyra*, the euphausiid *Meganyctiphanes norvegica*, the amphipod *Phronima sedentaria*, and the squid *Gonatus fabricii*. They correlated good catches of albacore with many *E. bispinosa* and *S. saurus* recovered from the stomachs. Le Danois (1921, 1922) related the feeding of albacore with the presence of the amphipod *E. bispinosa* in waters whose temperature, at a depth of 50 m., was not less than 14° C. He also found juvenile anchovy (*Engraulus encrassicholus*), horse mackerel (*T. trachurus*), saury (*S. saurus*), smelt (*Argentina* sp.), and lantern fish (*Myctophum* sp.) in albacore stomachs.

Legendre (1932, 1934, 1940) and Bouxin and Legendre (1936) have published the most detailed reports dealing with the food of albacore from the eastern North Atlantic. Legendre (1940), for example, summarizes the food of albacore from 1929 to 1933 in a list comprising 106 species from five phyla. The ten most important food items reported by Legendre were similar to the most important food items of albacore captured off California and Baja California (McHugh, 1952). Le Gall (1949) has reviewed the albacore food studies by French workers and noted the differences in stomach contents of fish taken over a period of almost 30 years.

SOURCE OF MATERIALS

A total of 544 albacore stomachs were examined. They were collected on 24 cruises of the *Hugh M. Smith*, *Charles H. Gilbert*, and *John R. Manning*, during the years 1950–57. The data for the 24 cruises are summarized in table 1 and the overall collection area is shown in figure 1. Stomachs were taken from albacore captured by longlining, trolling, and gill net fishing. Murphy and Shomura (1953) have discussed the method of longline fishing used on these cruises, and construction details of the gear have been described by Mann (1955). Trolling procedures have been decribed by Shomura and Otsu (1956) and Graham (1957, 1959), and the use of gill nets and construction details were reported by Graham and Mann (1959).

These three different fishing techniques did not sample the same sizes of albacore, as the smaller ($\leq$85 cm.) fish were taken primarily by trolling and gill netting at the surface and the larger (>85 cm.) albacore were caught by the deeper

fishing longline. Length frequency distributions of the albacore from which stomachs were collected are shown in figure 2.

METHODS

The stomachs were removed as soon as possible after the albacore came aboard, but the time interval between the moment of capture by the fishing gear and removal of the stomach varied considerably. Stomachs of troll-caught fish were removed immediately after capture, while the stomachs of some fish caught by longline or gill net were undoubtedly not removed until several hours had elapsed between the hooking or gilling of the fish and the hauling of the gear.

Of the 544 stomachs examined, the contents of 196 were analyzed at sea during *John R. Manning* cruise 36. This analysis consisted of measuring the total displacement volume ($\geqq$ 5cc.) of each stomach's contents and recording the numbers or presence of the following food groups: squid, saury (*Cololabis* sp.), other fish, shrimp-like plankton, copepod-amphipod-like plankton, and unidentifiable remains.

The other 348 stomachs were preserved for examination in the laboratory by placing them in muslin bags, along with any regurgitated material

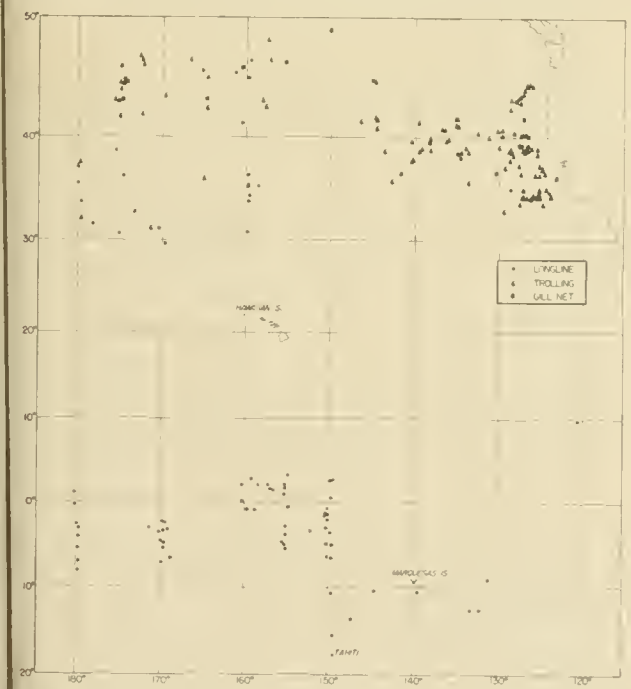

FIGURE 1.—Locations where stomach samples were taken from albacore captured by longline, gill net, and trolling in the central and northeastern Pacific, 1950–57.

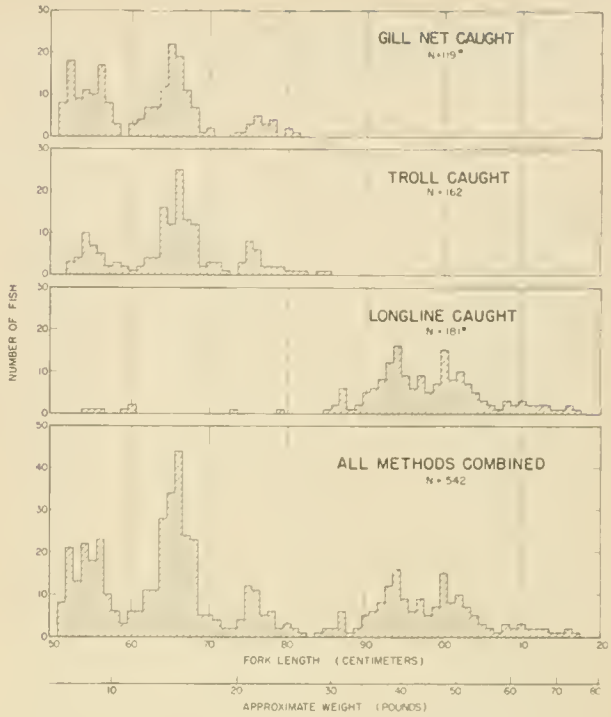

FIGURE 2.—Length frequency distributions of albacore tuna from which stomachs were collected. (Asterisk indicates one shark-mutilated specimen not included.)

recovered, in 10 percent formalin. Collection data, including vessel, cruise number, locality, date, fork length, time of capture if known, method of capture, bait species, and the observer's initials, were recorded on a cloth label which was placed in the muslin bag with the stomach.

In the laboratory the stomachs were soaked overnight in fresh water to remove excess formalin. The stomachs were then opened and the various food organisms separated according to species or to whatever taxon the precision of identification permitted. The number of individuals in each species or group was counted, and their volume determined by the displacement of water in a graduated cylinder. Bait found in the stomachs of longline-caught albacore was excluded.

A checklist of food organisms from 348 stomachs analyzed in the laboratory appears in the Appendix table. The contents of the 196 albacore stomachs analyzed at sea have been reported by Graham (1959). In a number of instances the data obtained from these two groups of stomachs could not be analyzed together due to the differences in the method of recording data.

Stomachs were randomly selected except on *John R. Manning* cruise 36, when 48 stomachs

TABLE 1.—*Albacore stomachs collected from the central and northeastern Pacific from 1950 to 1957 by vessels of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, according to cruise, time of year, locality, fishing method, and place of examination*

Vessel	Cruise number	Cruise period	Collecting area		Fishing method	Number of albacore captured	Number of stomachs examined	Percent of catch examined
			Range of latitude	Range of longitude				
Hugh M. Smith	5	June–Aug. 1950	3° S.	171° W.	Longline	4	2	50
Hugh M. Smith	11	Aug.–Oct. 1951	1° N.–2° S.	150° W.	do	4	4	100
John R. Manning	11	Jan.–Mar. 1952	3° N.–8° S.	155° W.–180°	do	64	22	65
John R. Manning	13	Oct.–Dec. 1952	2° S.–5° S.	152° W.–170° W.	do	22	6	27
John R. Manning	14	Jan.–Mar. 1953	1° S.–16° S.	144° W.–150° W.	do	40	25	62
John R. Manning	15	Apr.–June 1953	3° N.–7° S.	150° W.–170° W.	do	67	39	58
John R. Manning	16	July–Sept. 1953	3° N.–4° S.	155° W.–160° W.	do	21	15	71
John R. Manning	18	Nov.–Dec. 1953	5° S.	155° W.	do	2	1	50
John R. Manning	19	Jan.–Mar. 1954	31° N.–35° N.	160° W.	do	47	11	23
Charles H. Gilbert	15	Feb.–Apr. 1954	2° N.–9° S.	121° W.–155° W.	do	13	10	77
John R. Manning	20	May–June 1954	3° N.–0°	157° W.–160° W.	do	7	6	86
John R. Manning	22	Sept.–Nov. 1954	36° N.–46° N.	159° W.–175° W.	do	26	11	42
Charles H. Gilbert	17	Sept.–Nov. 1954	37° N.–45° N.	165° W.–172° E.	Trolling	48	16	33
John R. Manning	23	Dec. 1954–Feb. 1955	29° N.–36° N.	159° W.–180°	Longline	50	14	28
					Trolling	2	1	50
Hugh M. Smith	27	Jan.–Feb. 1955	32° N.–33° N.	173° W.–179° E.	do	2	2	100
John R. Manning	25	May–June 1955	36° N.	165° W.	do	1	1	100
Hugh M. Smith	30	July–Aug. 1955	46° N.–48° N.	157° W.	do	8	4	50
John R. Manning	26	July–Sept. 1955	35° N.–40° N.	128° W.–129° W.	Longline	6	1	17
					Trolling	64	1	2
Charles H. Gilbert	23	Sept.–Nov. 1955	41° N.–46° N.	145° W.–165° W.	Longline	1	1	100
					Trolling	66	10	15
					Gill net	11	8	73
John R. Manning	32	July–Sept. 1956	42° N.–49° N.	145° W.–175° W.	Trolling	104	11	10
					Gill net	498	46	9
Charles H. Gilbert	30	Aug.–Sept. 1956	9° S.–14° S.	132° W.–140° W.	Longline	26	13	50
Charles H. Gilbert	31	Oct.–Dec. 1956	34° N.–41° N.	125° W.–144° W.	Trolling	154	17	11
					Gill net	1	1	100
John R. Manning	33	Oct.–Dec. 1956	39° N.	130° W.	Trolling	79	1	1
John R. Manning	36	June–Aug. 1957	33° N.–45° N.	124° W.–143° W.	Longline	1	1	100
					Trolling	226	[1] 98	43
					Gill net	149	[2] 145	97

[1] Of this number, 83 were examined at sea.

[2] Of this number, 113 were examined at sea.

were chosen for analysis in the laboratory because they were thought to contain food. However, many of these stomachs were empty or nearly so, and it is considered that any bias introduced into the sampling was slight.

The reporting of results has followed the approach used by Reintjes and King (1953) and King and Ikehara (1956). This takes into account the number of organisms, the frequency of their occurrence, and their individual and aggregate total volumes. An expression used throughout this report is that of volume (in cc.) of stomach contents per pound of body weight of the individual fish. Since the capacity of an albacore's stomach depends upon the size of the fish, the comparison of the stomach volumes of large and small fish together would tend to bias the data in favor of the larger fish. Figure 3 shows the relationship between volume (cc.) per pound body weight and body weight. The points are somewhat scattered and are probably not normally distributed, but there is an indication of an overall decrease in average stomach content per unit of body weight with increase in fish size, a situation similar to that reported for yellowfin (*Neothunnus macropterus*) and bigeye (*Parathunnus sibi*) tuna by King and Ikehara (1956).

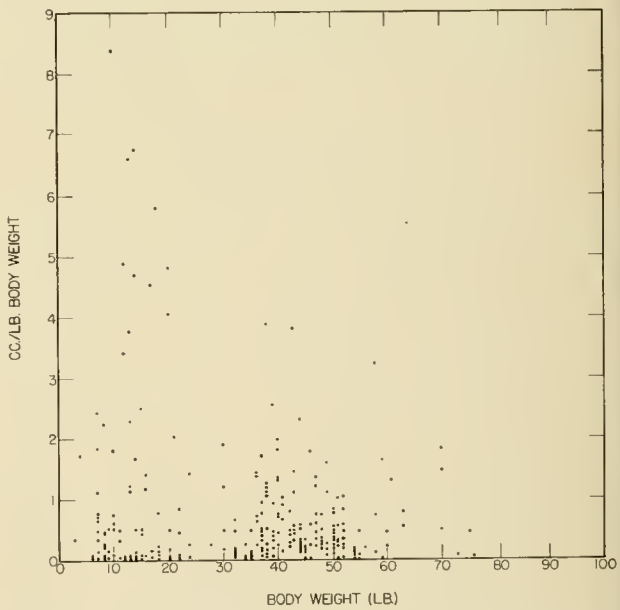

FIGURE 3.—Relationship between food volume per unit of body weight and total body weight of 260 longline- and troll-caught albacore tuna.

Gill net-caught albacore were not included in figure 3 since a high percentage of their stomachs were empty or nearly so, which may reflect the time of feeding or a variable introduced by the

fishing method. Where albacore of approximately the same size were considered, the average volume of food per stomach was also used as a basis for comparison. In some instances, weights of the albacore were estimated from length to weight tables developed at the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

Statistical tests of significance have not been made, for, as King and Ikehara (1956) pointed out: "Regardless of the mehods of analysis used, there are many uncontrollable variables inherent in food studies which detract from the precision of the results." There is evidence (Reintjes and King, 1953, fig. 4) that the parameters involved are not independent, and therefore the assumptions underlying the common tests of significance would be violated.

In a number of my comparisons of stomach content data with environmental variables, the stomach data represent catches made during different cruises and years. Little can be done to rectify this weakness, since further grouping of the stomach data into subclass numbers more discrete than those shown would produce subsamples of very small numbers.

RESULTS

VARIATION IN FOOD WITH FISHING METHOD AND SIZE OF THE ALBACORE

The following discussion of variations in the food of albacore with the method of capture by inference is a generalization on variations in food with albacore size, since the methods of capture sampled different size groups (fig. 2).

There are distinct differences in the average volume of food per stomach and in the composition of the foodstuffs depending upon which fishing method was used. Table 2 shows the average volume per stomach, figure 4 shows the distribution of these volumes, and figure 5 shows the comparative importance, by volume, of the major food groups of stomach contents, according to method of capture.

TABLE 2.—*Average stomach volumes of 348 albacore, according to method of capture*

Method of capture	Number of stomachs	Average volume (cc.) per stomach
Longline	182	26.7
Gill net	87	9.8
Troll	79	15.1

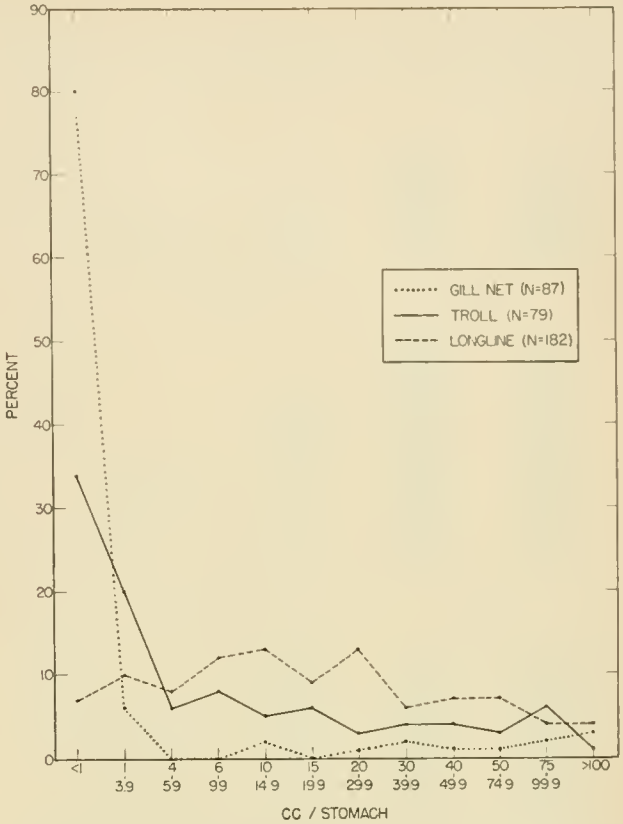

FIGURE 4.—Distribution of stomach content volumes of 348 albacore, according to method of capture.

The higher average volume per stomach of the longline-caught albacore is undoubtedly due to their larger sizes, since the longline captured all the albacore longer than 85 cm. Only 9 percent of the longline-caught fish were under 85 cm. while the majority of the gill net- and troll-caught albacore were in the 50–70 cm. range.

The difference in average stomach volume between the troll- and gill net-caught fish is not as easily explained, since the fish of both groups were approximately the same size. One possibility is that this difference reflects the time of feeding of albacore, because the troll-caught fish are taken during the day and the gill netted albacore are thought to have been caught at night, even though the gill net is hauled aboard after dawn. An indication of this was provided by the 24-hour gill net station on *John R. Manning* cruise 36. No albacore were caught by the sets made from 0828 to 1531 hours and from 0230 to 0942 hours. Seventeen were caught by the set from 2003 to 0358 hours, and 6 albacore were caught in the set from 1502 to 2153 hours

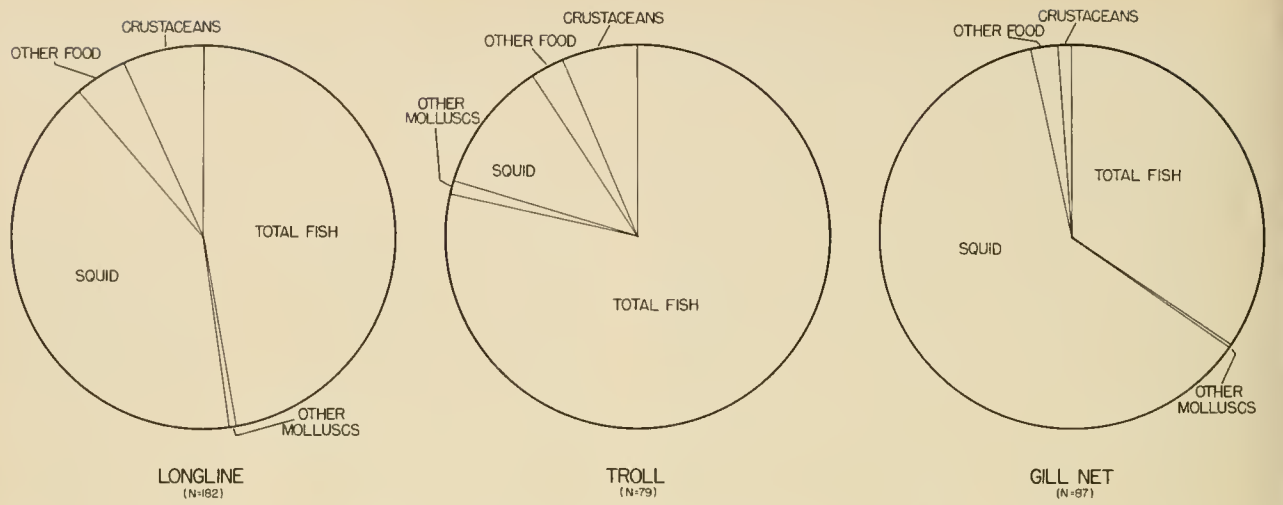

FIGURE 5.—Comparative importance, by volume, of major food elements found in 348 albacore stomachs, according to method of capture.

(Graham, 1959). Another possibility is that the gill net-caught fish regurgitated food while struggling to escape the net. A third possibility is that albacore do feed at night, but at a reduced rate. These suggestions are discussed more fully in the section dealing with feeding related with time of day.

Differences among the aggregate total volumes of major food items of albacore captured by trolling compared with longline-caught and gill netted fish are evident (fig. 5). Fish and squid formed approximately equal portions of the food of longline-caught albacore, while fish comprised 79 percent and squid comprised 11 percent of the diet of troll-caught albacore. This agrees with McHugh's data (1952), which showed fish as 68 percent and squid as 12 percent of the food volume of troll-caught albacore. In both cases saury, *Cololabis* sp., comprised the bulk of the fishes. Reintjes and King (1953) also found fishes to form a larger portion of the diet of troll-caught yellowfin tuna when compared with longline-caught yellowfin in both the Line Islands and Phoenix Islands areas.

Perhaps the trolling method, which employs a lure skipping and plunging along a few feet below the surface, may especially attract albacore previously conditioned by a diet of fish having the gross characteristics of a trolling lure. If this is true, and there were numbers of albacore in the trolling area which had been feeding on organisms (e.g. crustaceans) which do not have these characteristics, a portion of the available albacore might not be efficiently exploited. Joubin and Roule (1918), however, found that amphipods were the main food of troll-captured albacore in the Gulf of Gascony.

Yuen (1959) has pointed out that the feeding behavior of skipjack tuna (*Katsuwonus pelamis*) may be conditioned by previous feeding. He hypothesized that livebait fishing methods used in Hawaii take advantage of an already existing feeding excitement in the skipjack.

The frequency of occurrence of major food groups is shown in figure 6. Differences between the longline and gill net-caught fish are large, but even if the gill net data are considered atypical, there are still substantial differences between longline- and troll-caught fish. The spread between values for these two groups for three classes of food are as follows: squid, 35 percent; fish, 27 percent; crustaceans, 24 percent. It may be simply that the larger, longlined fish require more food than the smaller, troll-caught albacore and thus would be apt to have more types of food in their stomachs. Possibly the reason squid and fish dominate in gill netted albacore is that their hard parts (squid beaks and eye lenses and fish vertebrae) remain in the stomachs after other organisms have been completely digested.

Representatives of 32 fish families and 11 invertebrate orders were found in the food of longlined albacore, compared to 9 fish families and 10 invertebrate orders for troll-caught and 4 fish families and 5 invertebrate orders for gill net-caught albacore. The most frequently occurring fish families in the longlined albacore were Gempylidae,

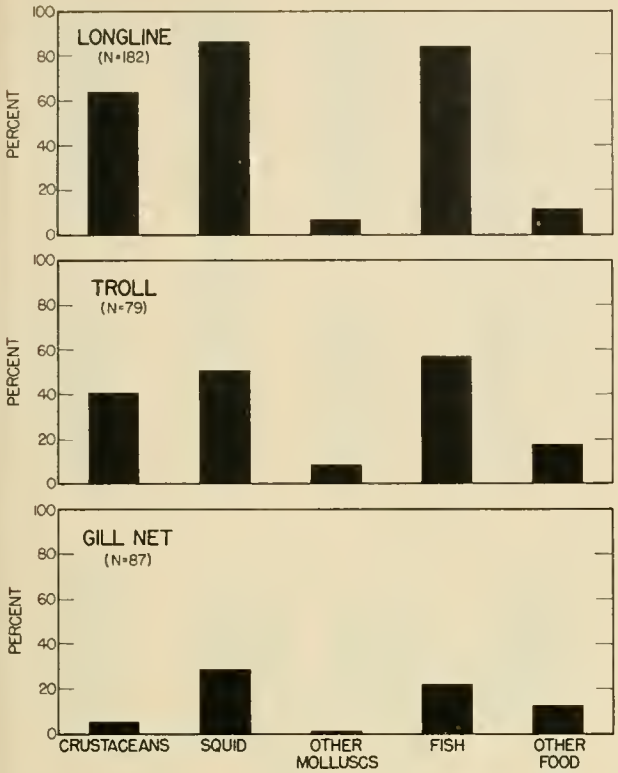

FIGURE 6.—Frequency of occurrence of major food groups in 349 albacore according to method of capture.

Bramidae, Sternoptychidae, Paralepididae, Myctophidae, Scomberesocidae, Chiasmodontidae, and Alepisauridae. Saury dominated in troll- and gill net-caught albacore, with myctophids next in frequency of occurrence. Squid were well represented in the albacore captured by all three methods.

Among the crustaceans, the main difference was the lack of stomatopods in the diet of troll- and gill net-caught albacore. This reflects the scarcity of stomatopods in the offshore plankton in the temperate North Pacific. For example, during *Hugh M. Smith* cruise 30, which covered the area north of Hawaii to approximately latitude 50° N., stomatopods occurred in only 2 of 124 plankton samples collected. These two samples were collected at 25° N. and 30° N., on the southern portion of the cruise.

VARIATION IN FOOD WITH LATITUDE AND LONGITUDE

Latitudinal variations in the volume of the food of longline-captured albacore from the equatorial Pacific are compared with variations in zooplankton, larger trawl-caught organisms, and the catch rate of albacore in figure 7.

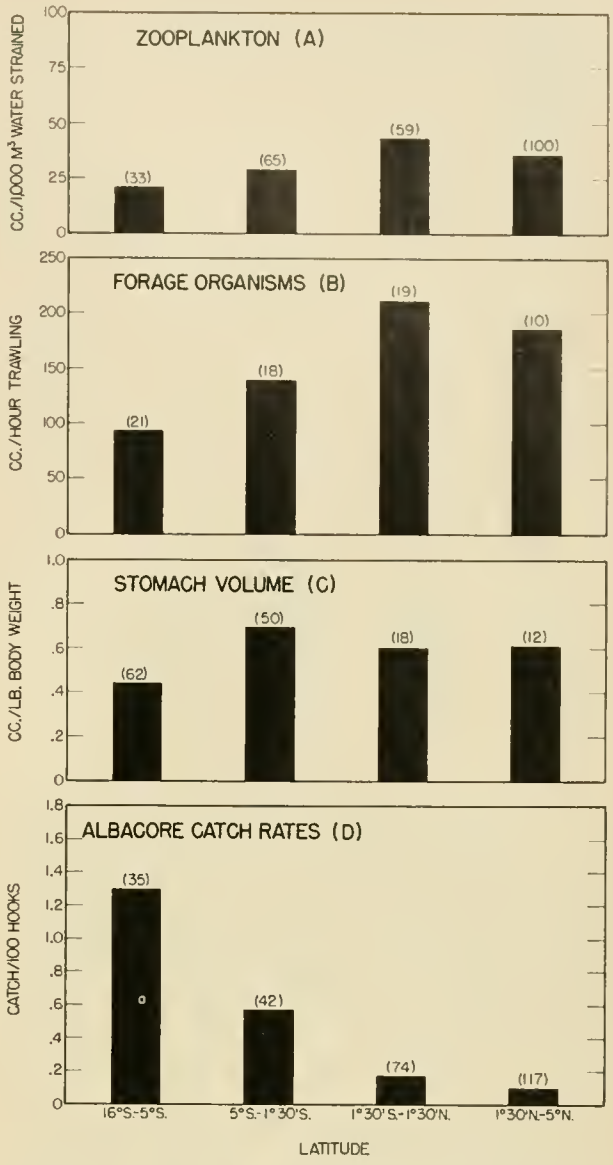

FIGURE 7.—Latitudinal variations in the equatorial Pacific of (A) zooplankton, (B) forage organisms, (C) volume of stomach contents per pound body weight of 142 longline-caught albacore, and (D) albacore catch rates. (Numbers in parentheses refer to sample sizes or (D) number of longline fishing stations.) Zooplankton data from King and Hida, 1957. Forage organism data from King and Iversen, 1962. (Catch rate data from the records of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.)

The method used by King and Hida (1957), presenting data on zooplankton abundance in the equatorial Pacific according to the subdivisions of the equatorial current system, has been followed in constructing figure 7. In this report the subdivisions utilized are: (1) a zone of convergence in the

westward-flowing South Equatorial Current (SEC) from approximately 5° N., to 1½° N.; (2) a zone of upwelling in the SEC from 1½° N. to 1½° S.; (3) the SEC from 1½° S. to 5° S., an area with a deep thermocline; and (4) the SEC from 5° S. to 16° S., the southern limit of sampling and a region of shoaling thermocline towards the south. This representation of the SEC does not take into account Reid's (1959) report of a weak easterly countercurrent near 10° S.

Values for zooplankton and trawl-caught organisms (small nekton for the most part) were highest near and just north of the Equator, where the abundance of albacore was lowest. The assumption has often been made that, all other things being equal, areas with the higher concentrations of zooplankton and small nekton should support the higher concentrations of large carnivores, such as albacore. The fact that this assumption is not supported by the data shown in figure 7 probably means that environmental factors other than the abundance of available food, such as water temperature, exert a strong influence on albacore distribution.

Whether or not the albacore captured in the areas of high zooplankton and nekton abundance were utilizing available forage to best advantage is not clear from figure 7, since the total range of stomach volumes was only 0.4–0.7 cc./lb. of body weight. The lowest stomach volumes occurred in the latitudes of best albacore catches, a situation similar to that found for yellowfin tuna in the equatorial area (King and Ikehara, 1956). One factor which adds to the uncertainty is that the trawling upon which the values shown in section B of figure 7 are based was done at night and many of the animals captured are not utilized by tunas as forage (King and Iversen, 1962). However, King and Iversen also found a high positive correlation between trawl catches and zooplankton abundance, and the assumption that trawling results are a valid estimate of potential tuna forage should not be dismissed, since some animals that make up a considerable portion of the trawl catches (e.g. myctophids) are actively pursued by animals which make up a large fraction of albacore food, such as squid.

The utilization of forage was further investigated by examining the occurrence and amounts of squid, fish, and crustacea in the diet of equatorial albacore. The results are shown in figures 8 and 9.

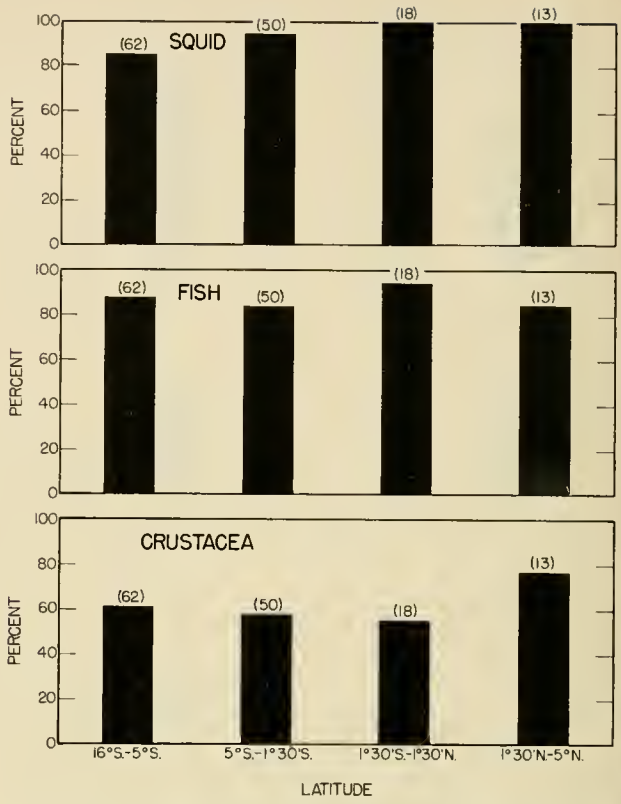

FIGURE 8.—Percent occurrence of major food items in the diet of equatorial longline-caught albacore, 120° W.–180°. (Numbers in parentheses indicate sample sizes.)

Squid occurred more often and in larger amounts than fish in the stomachs of albacore taken from 1½° S. to 5° N. This is contrary to the findings of King and Ikehara (1956), who found that fish formed overall a larger portion of yellowfin and bigeye food in equatorial waters than did squid.

There were also differences in the fish consumed by longline-caught albacore in the equatorial Pacific when compared to longline-caught albacore from the temperate North Pacific (table 3). It is puzzling that no bramids or gempylids were found in the stomachs of longline-caught albacore from the temperate North Pacific, since species of both families occur in this area. It may be that bramids and gempylids are distributed close to the surface in the north and in deeper water in the equatorial area. In such a case they would not be as available to the albacore fished with longlines in the north as they would be to the albacore exploited by the same gear in equatorial waters. A possibly analogous tropical submergence or deepening of

habitat with decrease in latitude has been demonstrated for the great blue shark (*Prionace glauca*) in the central Pacific by Strasburg (1958).

TABLE 3.—*Percent occurrence of fishes prominent in the diet of longline-caught albacore, according to area of capture*

Family	Area of capture	
	Equatorial Pacific	Temperate North Pacific
Gempylidae	28.5	
Bramidae	21.5	
Scomberesocidae		18.4
Sternoptychidae	8.3	10.5
Myctophidae	4.2	5.3
Alepisauridae	2.1	5.3
Paralepididae	4.9	2.6
Chiasmodontidae	4.2	
Number of stomachs examined	143	38

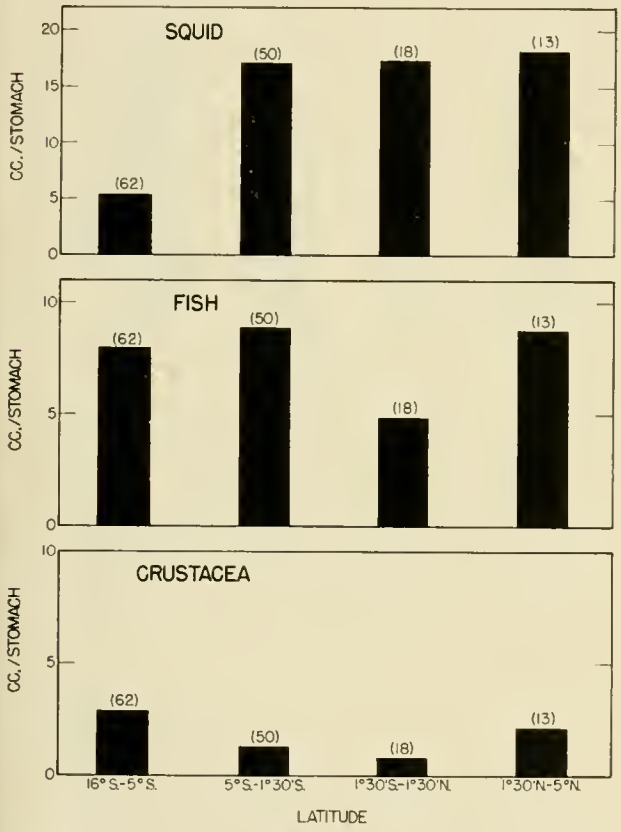

FIGURE 9.—Variation (cc./stomach) of major food items in the diet of equatorial longline-caught albacore, 120° W.–180°. (Numbers in parentheses indicate sample sizes.)

Latitudinal variations in the temperate North Pacific for zooplankton, forage organisms obtained by midwater trawling, and volumes of the stomach contents of longline- and troll-caught albacore are shown in figure 10.

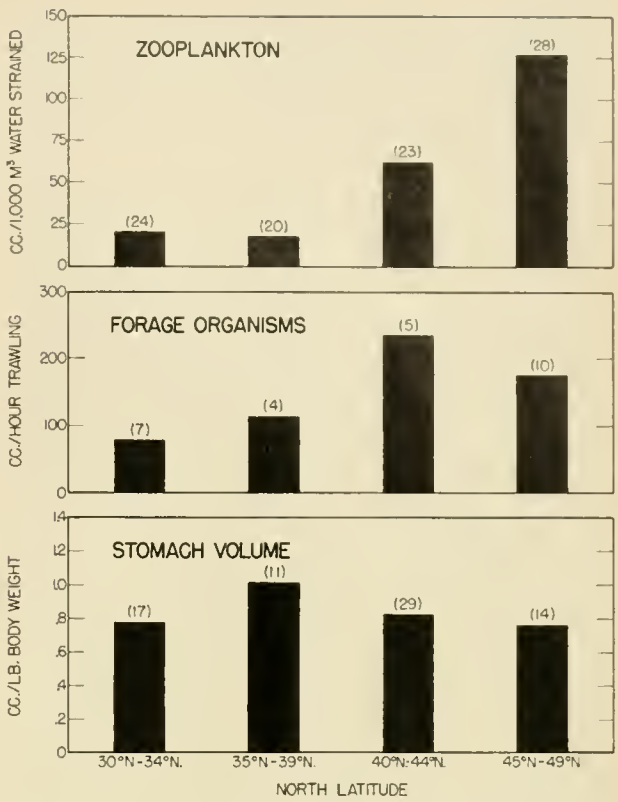

FIGURE 10.—Latitudinal variations in the temperate North Pacific (140° W.–180°) of zooplankton, forage organisms, and in the volume of stomach contents per pound of body weight of 71 albacore caught by longline and trolling. (Numbers in parentheses refer to sample sizes. Data obtained during summer and fall cruises, except for stomach volumes from 30°–34° N., which were obtained in winter. Zooplankton data from McGary, Jones, and Austin, 1956. Forage organism data from King and Iversen, 1962.)

It appears from figure 10 that zooplankton volumes are highest to the north, trawling volumes are highest south of the zooplankton peak, and the albacore stomach volumes are highest south of the peak trawling volumes—indications of what may be the development of successive trophic levels.

McGary, Jones, and Graham (1958) have shown the existence of a "Transition Zone" in the central North Pacific between the Central Water Mass and the Subarctic Water Mass. This Transition Zone, which has temperature-salinity qualities intermediate between those of the Central and Subarctic Water Masses, is characterized by a northward movement of the isotherms starting in the spring as the surface layer is warmed and a marked thermocline develops. In the summer the northern limit of the warmed surface layer is at about

47°–48° N. McGary, Jones, and Graham state: "The frontier of this warming layer apparently offers optimum conditions for a phytoplankton bloom followed by an increase in zooplankton abundance."

As such a "frontier" with an associated trophic level (zooplankton, for example) moves northward, one might expect it to be followed by other trophic levels, each successively exploiting the one preceding it. In this case (fig. 10) it is postulated that zooplankton are exploited by forage organisms which are most abundant south of an advancing frontier of high zooplankton abundance. The forage organisms (saurics and squid, not necessarily those captured by midwater trawling) are in turn exploited by the albacore, and the largest stomach volumes are found to the south of the area of highest trawling volumes.

The consumption of food by albacore captured by troll and longline from 120° W. to 140° W. and from 140° W. to 180° during summer and fall in the temperate North Pacific is compared with the abundance of zooplankton in these two areas in figure 11. Such a comparison provides another estimate of the utilization of forage by albacore, although the zooplankton is usually considered two trophic levels removed from the albacore.

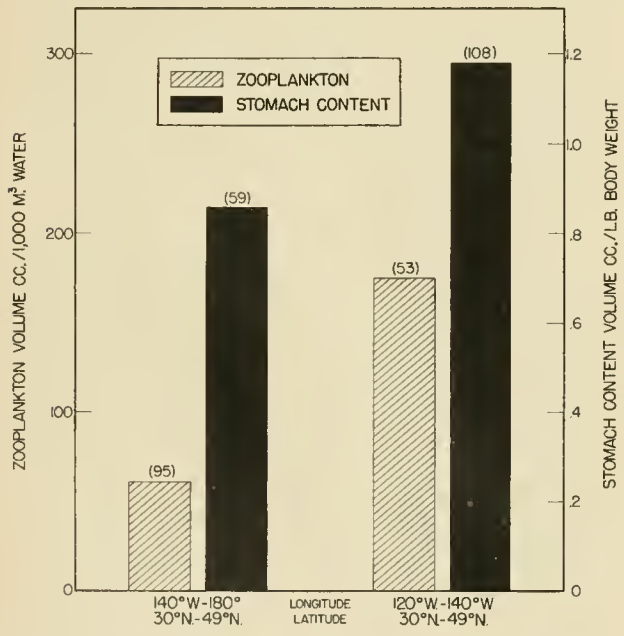

FIGURE 11.—Stomach content volumes of albacore captured by troll and longline and zooplankton volumes from the temperate North Pacific. Plankton data from McGary, Jones, and Austin, 1956, and Norpac Committee, 1960. (Numbers in parentheses refer to sample sizes.)

Albacore captured at 120° W.–140° W. had more food in their stomachs than albacore captured at 140° W.–180°, even though the data upon which figure 11 is based favor the latter. This bias occurs because most of the fish captured at 120° W.–140° W. were examined in the field and only stomach content volumes of 5 cc. or greater were recorded. In the construction of figure 11, any field-examined stomach with less than 5 cc. was considered empty, while values from 0 to 5 cc. were recorded for stomachs examined in the laboratory. It appears, therefore, that albacore captured at 120° W.–140° W. were utilizing the larger amount of food available to them, as indicated by the higher zooplankton volumes recorded at 120° W.–140° W.

East-west variations in stomach content volumes of longline-caught albacore in the central equatorial Pacific are compared with zooplankton volumes in figure 12. These differences may reflect the east-west variation in the equatorial circulation and tend to support the hypothesis advanced by King and Iversen (1962) that decreasing zooplankton abundance from east to west in the equatorial Pacific may be related to predation by an expanding population of forage organisms. The latter in turn are eaten by climax predators, such as albacore. This is indicated by the high stomach content volumes recorded near 180°. As newly upwelled water from the eastern Pacific is carried westward, the inorganic phosphate present decreases, the temperature increases, and the thermocline deepens (Austin, 1958). The decrease in inorganic phosphate presumably indicates an increase in organic production by expanding populations of phytoplankton and zooplankton. However, such an increase in the abundance of zooplankton from east to west is not shown by the data (fig. 12), and it is to explain this phenomenon that the importance of predation by forage organisms has been suggested. King and Iversen (1962) have reported the amount of forage organisms captured by midwater trawling to be higher at 140° W.–160° W. than at 110° W.–140° W., indicating a westward increase in such predators, many of which depend upon zooplankton as food.

The volumes of albacore stomach contents also parallel somewhat the east-west variation in stomach volumes reported by King and Ikehara (1956) for the bigeye tuna of the equatorial Pacific, which like the albacore also inhabits the

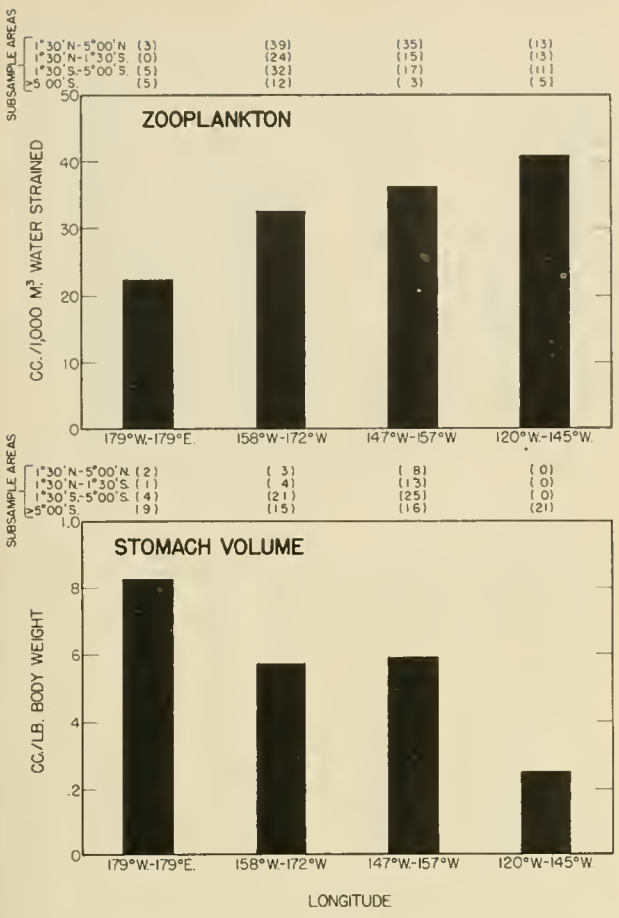

FIGURE 12.—Longitudinal variations in the equatorial Pacific of zooplankton and the volume of stomach contents per pound body weight of 121 longline-caught albacore. (Numbers in parentheses refer to sample sizes.) Zooplankton data are from King, Austin, and Doty (1957) and King and Hida (1957) and have been adjusted to remove the effect of diurnal variation according to the method of King and Hida (1954).

deeper waters. The highest bigeye stomach content volumes occurred in the western part of the sampling area (155° W.–180°).

VARIATION IN FOOD WITH SEASON

Seasonal variation in the food of 78 albacore troll- or longline-caught in the temperate North Pacific between 140° W. and 180° is shown in table 4. Summer and fall samples were combined, since most of the samples were obtained during the end of summer and beginning of fall. There is little difference between the summer-fall and winter values, although the range of sampling was 10° of latitude broader in summer than in winter.

TABLE 4.—*Seasonal variation in food of troll- and longline-caught albacore from the temperate North Pacific, 140° W.–180°*

	Summer and fall (30° N.–49° N.)	Winter (30° N.–39° N.)
Volume in cc./lb. body weight	0.85	0.79
Number of samples	54	24

Seasonal variation in the food of 143 albacore taken by longlining in the equatorial Pacific is shown in figure 13. From January through September the amounts of squid and fish per stomach do not vary greatly, but from October through December the amount of squid consumed approximately doubles. This may be due to the smallness of the sample. If we disregard the October through December results as a vagary of sampling, the next highest values were recorded for the April through June period, which agrees fairly well with the results shown by King and Ikehara (1956) for bigeye tuna in the equatorial Pacific, although their sampling period was from April through July.

VARIATION IN FOOD WITH DISTANCE FROM LAND

An examination of data on albacore stomach contents in terms of the distance of the point of capture from the nearest emergent land was un-

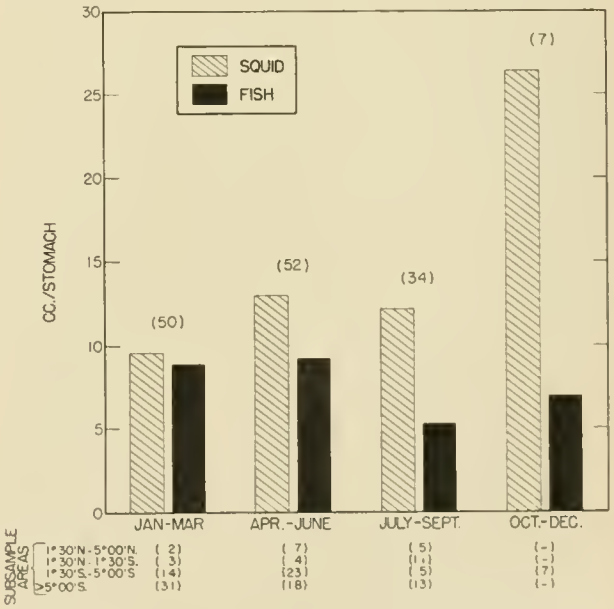

FIGURE 13.—Variation in the amount of squid and fish in the stomach contents of 143 albacore captured by longline in the equatorial Pacific, according to season. (Numbers in parentheses refer to sample sizes.)

dertaken only for the fish captured in the equatorial Pacific. Results are shown in figure 14. Samples from the temperate North Pacific were not included because: (1) no stomachs were collected from fish captured in the categories 0–24 and 25–99 miles from land, and (2) the fish from which stomachs were collected in the temperate North Pacific were much smaller, on the average, than fish captured in the equatorial Pacific.

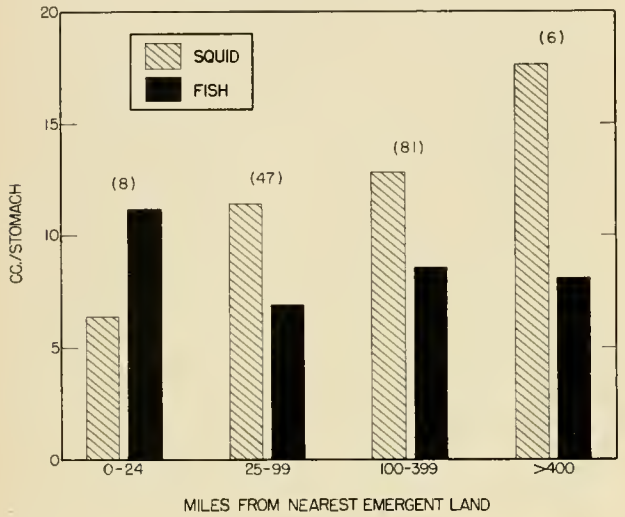

FIGURE 14.—Variation in food of 142 albacore captured by longline in the equatorial Pacific, according to distance from nearest emergent land. (Numbers in parentheses refer to sample sizes.)

Although two of the categories of figure 14 (0–24 miles and >400 miles) are based on small samples, the indication is that consumption of squid increases in an offshore direction. The percent occurrence of squid was as follows: 0–24 miles, 64 percent; 25–99 miles, 94 percent; 100–399 miles, 95 percent; >400 miles, 83 percent. King and Ikehara (1956) found generally similar results for the volume and percent occurrence of squid in the stomach contents of longline-caught bigeye in the equatorial Pacific, although they had no samples in the 0–24 miles category. This may reflect an offshore increase in the abundance of the deeper swimming squids in this area. The consumption of fish was highest in the 0–24 miles category, with lower, fluctuating values noted as distance increased away from land.

The appearance of reef-associated organisms in the diet of equatorial albacore, as might be expected, reflects the distance from land at the place of the albacore's capture. Their appearance is summarized in table 5. The indication is that fewer reef-associated organisms are eaten by albacore as distance increases offshore, presumably a reflection of the diminishing abundance of such organisms. This is further evidence that albacore are opportunistic feeders, taking whatever prey is available within broad food categories, an opinion expressed by several other writers on the subject.

TABLE 5.—*Percent occurrence of reef-associated organisms found in the stomach contents of albacore captured on longline in the equatorial Pacific, according to distance from nearest emergent land*

Organism	Miles from nearest land			
	0–24	25–99	100–399	>400
Crustacea:				
Larval Stomatopoda	50	40	16	
Crab megalopa	12	13	2	
Phyllosoma		2	1	
Homaridae				
Enoplometopus sp., postlarvae		8	2	
Palinuridae,[1] postlarvae		2		
Scyllaridae,[1] postlarvae		2		
Fish:				
Synodontidae [1]		2		
Holocentridae [1]		2	1	17
Holocentrus sp			1	
Apogonidae				
Cheilodipterus sp		2		
Carangidae [1]		2		
Chaetodontidae [1]	12	4	1	
Acanthuridae [1]		6	1	
Scorpaenidae [1]		2	1	
Scorpaena sp				17
Balistidae [1]		2		
Ostraciontidae [1]			1	
Lactoria diaphanus				17
Tetraodontidae [1]		2		
Number of stomachs examined	8	47	82	6

[1] Unidentified.

VARIATION IN FOOD WITH TIME OF DAY

In order to examine the trend of feeding throughout the day, stomach volumes of albacore caught by trolling during five summer cruises in the temperate North Pacific were combined and plotted by 2-hour periods corresponding to the local zone time when the albacore were captured. Results are shown in figure 15. Stomachs from longline-caught albacore were not included, since the exact time of their capture could not be determined. Stomachs examined in the field during *John R. Manning* cruise 36 were included to increase the sample size. Forty percent of these field-examined stomachs were designated empty, since only values of 5 cc. or larger were recorded in the field. However, since figure 4 shows that 34 percent of all laboratory-examined stomachs had volumes less than 1 cc., a percentage reasonably close to the 40 percent of the field-examined stomachs designated empty, these stomachs were included.

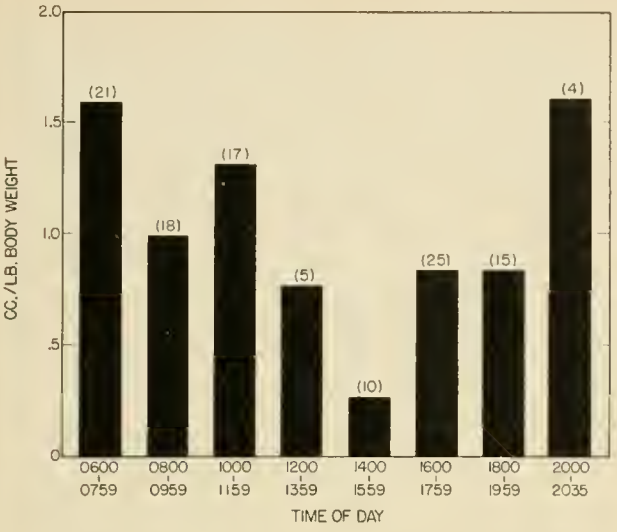

FIGURE 15.—Variation in stomach content volumes of 115 albacore caught by trolling in the temperate North Pacific during summer, according to time of day when captured. (Numbers in parentheses refer to sample sizes.)

Evaluating figure 15, one may say that while feeding takes place throughout the day, two general feeding periods are indicated—one in the early morning and another towards evening. The evidence for such an interpretation gains additional weight if the high value recorded for the 1000–1159 period is considered a sampling artifact, since one albacore accounts for 40 percent of the total value shown for that period.

Feeding periods have been reported by Uda (1940) and Nakamura [2] for skipjack tuna (*Katsuwonus pelamis*). Uda states that off Japan skipjack feed most actively in the early morning, again around noon, and presumably again near sunset. Nakamura found skipjack caught near the Marquesas Islands to be heavy feeders in the morning around 0900 hours, with little feeding around noon and another period of heavy feeding before sunset. The data shown in figure 15 more closely resemble conditions described by Nakamura for skipjack than those reported by Uda. As Nakamura points out, this probably reflects the lessened availability of tuna forage due to the downward daytime migration of zooplankton, the prey of much tuna forage.

The consumption of saury and squid throughout the day was examined and the results are given in table 6, which allows a comparison with McHugh's (1952) data on diurnal variation in albacore food. For hourly periods when at least 10 stomachs were sampled, percentages were calculated when either saury or squid were dominant in the stomachs. The results generally agree with McHugh's in that saury dominated frequently throughout the day and squid did not dominate as frequently in the early morning and late afternoon hours as they did during other times of the day.

Circumstances of the catch of the four specimens in the period from 2000 to 2035 hours (fig. 15), in which lighting conditions were approaching total darkness, lead to a discussion of whether or not albacore feed at night, a question briefly alluded to earlier in this report. Three of these four albacore stomachs contained food in the following amounts: 40 cc., 15 cc., and 7 cc.

TABLE 6.—*Percentage of troll-caught albacore stomachs in which either squid or saury was the dominant food organism, according to time of capture*

[Data given only for hourly intervals when 10 or more stomachs were sampled]

	Time of capture						
	0600–0659	0700–0759	0900–0959	1100–1159	1600–1659	1700–1759	1900–1959
Food:							
Squid	0	10	27	9	21	9	8
Saury	27	40	36	18	21	27	25

Stomach volume data (table 2) from gill netted albacore show that there was, on the average, much less food in such stomachs than in the stomachs of longlined or troll-caught albacore. Since the gill net was fished at night, this difference suggests that albacore may feed less during the hours of darkness. By the nature of the gear, however, longlines and trolling lures are probably selective for actively feeding fish, while the passive gill net would take albacore which were not feeding. There is also a possibility that gill netted albacore regurgitate their stomach contents, but the high percentage of typically empty stomachs (with a narrow lumen and deeply convoluted rugae) in such fish makes this seem unlikely.

There is indirect evidence, discussed below, which indicates that albacore probably do feed at night. This conclusion is supported by the fact that some food has been found in the stomachs of albacore taken in night gill net fishing. The success of nighttime as compared with daytime feeding is difficult to estimate because of the selectivity of the different fishing methods.

[2] Nakamura, E. L., Food and feeding habits of Marquesan skipjack (*Katsuwonus pelamis*). MS., Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

Watanabe (1958) states that both bigeye and yellowfin feed at night, with the bigeye the more active feeder. He did not report on albacore. Matthews [3] conducted a histological examination of the retinas of yellowfin, bigeye, skipjack, and albacore. Among yellowfin, bigeye, and skipjack he found little evidence of differences in visual potentialities. According to Matthews: "The albacore are quite another problem. Here are retinas with cone potentials probably equal to those of skipjack, yellowfin, and bigeye tuna, but in addition, from the evidence I have observed, possess a greater development of their rods. This may account for the fact that they are frequently taken in turbid waters. . . ." He also stated that "One can say that in the albacore there are at least twice as many if not more rods than twin cones."

Since the rods are used for night vision, it appears that albacore have retinas with a capability for a comparatively keener vision at night or under conditions of low illumination. Ikeda's (1958) report of a luminous lure used at night by Japanese longline fishermen that "is especially good for albacore fishing" would tend to bear this out. The descents of Beebe (1934) and others attest to the amount of bioluminescence in the oceans. Myctophids, euphausiids and other kinds of crustaceans, and many cephalopods are noted for luminosity (Marshall, 1954). Even fishes or crustaceans which are not luminous may leave a luminous trail as they swim through waters inhabited by peridinians and other kinds of dinoflagellates (Harvey, 1952). An albacore with a theoretical capability of nighttime vision might be able to spot these luminous trails and track down its prey.

VARIATION IN FOOD WITH WATER CLARITY

In his paper on the effect of water clarity on albacore catches, Murphy (1959) considered the abundance of albacore as it is related to turbidity, a function of the amount of particulate matter in the ocean. He theorized that dense concentrations of phytoplankton might obscure available tuna forage from sight feeders, such as the albacore, which then might temporarily leave an area that had prior to the phytoplankton increase a forage concentration sufficient to sustain them.

[3] Matthews, D. C., A comparative histological study of the retinae of skipjack (*Katsuwonus pelamis*), yellowfin (*Neothunnus macropterus*), bigeye (*Parathunnus sibi*), and albacore (*Germo alalunga*) tuna. Manuscript, Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

In order to investigate the effect of water clarity on the amount of forage present in the stomachs of troll-caught albacore, stomach volumes were plotted against the depth of Secchi disc observations made during eight cruises to the temperate North Pacific. The results are shown in figure 16. Secchi disc observations were used rather than light penetration measurements made by a photometer because for some cruises only Secchi disc readings were available. Also, Clarke (1941) and Graham and Gooding,[4] have shown there is good agreement between observations made simultaneously with both the Secchi disc and the photometer. Secchi disc observations were made either once or twice a day while the vessels were running between stations. When more than two observations were made on the same day the observation made closest to the place of capture of the albacore was used.

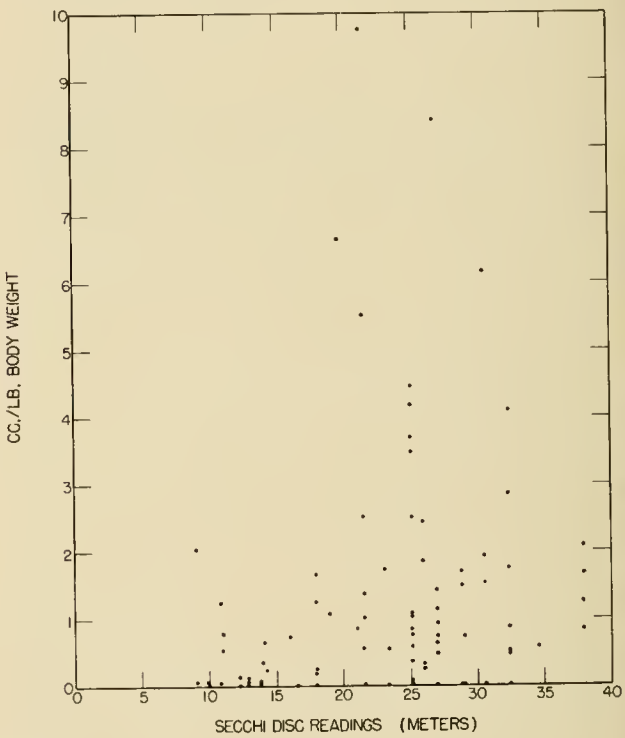

FIGURE 16.—Variation in the volume of stomach contents per pound body weight of 111 albacore caught by troll in the temperate North Pacific, according to Secchi disc readings.

The points shown in figure 16 for stomach volumes up to 3 cc./lb. body weight are fairly

[4] Graham, J. J. and R. M. Gooding, Northeastern Pacific Albacore Survey. Manuscript, Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

well scattered throughout the range of Secchi disc readings, but the higher values for stomach contents are found in the mid-range of light penetration values, with the highest value recorded at a Secchi disc reading of approximately 22 meters.

An inference that can be made from figure 16 is that while foraging does take place in waters which vary considerably in clarity, the most successful foraging may take place in waters which represent a compromise between (1) heavy standing crops of tuna forage in waters of low clarity and (2) conditions of excellent visibility but where the amount of tuna food is less.

COMPETITION FOR FOOD AMONG ALBACORE, YELLOWFIN, AND BIGEYE TUNA

An investigation was made to determine whether albacore compete for food with yellowfin and bigeye tuna in the equatorial Pacific, since the three species are caught in this general area. King and Ikehara (1956) made an extensive comparative study of the food of yellowfin and bigeye from the equatorial Pacific and reported: "Despite the differences we have pointed out, the foods of yellowfin and bigeye are remarkably similar. We conclude, therefore, that when occupying the same general area the two species have the same feeding habits."

The taxonomic categories they found in the food of yellowfin and bigeye are compared in table 7 with those found in albacore stomach contents. Table 7 shows that fewer taxa in every category except one were found in albacore stomachs than either yellowfin or bigeye stomachs. However, more than twice as many yellowfin stomachs and 23 percent more bigeye stomachs were examined than albacore stomachs, which lessens the weight of evidence indicating more omnivorous feeding by the yellowfin and bigeye. Also, most of the yellowfin and bigeye studied by King and Ikehara were considerably larger than the albacore with which they are compared. One might expect a larger yellowfin or bigeye, requiring a greater daily ration than an albacore, to eat a greater variety of organisms while foraging. The overall similarities in the diets of yellowfin and bigeye are compared with albacore in table 7. Except in two cases, over half the taxa found in albacore stomachs were reported in the food of yellowfin and bigeye.

TABLE 7.—*Numbers of certain taxonomic categories represented in the food of albacore, yellowfin, and bigeye tuna taken on longline more than 25 miles from land in the equatorial Pacific*

[Figures in parentheses are numbers of such categories common to yellowfin or bigeye and albacore. Data on yellowfin and bigeye food from King and Ikehara (1956)]

Species	Invertebrates			Vertebrates (Pisces)		Number of stomachs examined
	Orders	Families	Genera	Families	Genera	
Albacore	10	20	12	30	21	135
Yellowfin	12(8)	31(14)	30(9)	48(24)	52(12)	439
Bigeye	9(6)	22(9)	17(3)	36(18)	38(8)	166

Table 7 does not provide, however, a comparison based on a restricted geographical area. Such data, available for cruise 11 of the *John R. Manning*, are given in tables 8 and 9, which compare the stomach contents of albacore with yellowfin and bigeye caught at the same location. In these instances, the food of albacore more closely resembled that of yellowfin than of bigeye, although the albacore is thought to inhabit, with the bigeye, deeper waters than the yellowfin in the equatorial Pacific. Nevertheless, the similarities in diet between both the albacore and the yellowfin and albacore and the bigeye in the same specific location, as well as in the same general area, are evidence that there may be some competition between the albacore and the other two species of tuna.

SUMMARY

1. This report is based upon the analysis of the stomach contents of 544 albacore tuna captured by longline, gill net, and troll fishing during 24 cruises by vessels of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, from 1950 to 1957.

2. Albacore from which stomachs were examined were captured in the equatorial and temperate zones of the central and northeastern Pacific. The limits of the sampling area were approximately latitude 16° S. to 49° N. and longitude 121° W. to 172° E.

3. Troll- and gill net-caught albacore from which stomachs were examined were 51–85 cm. in fork length, while longline-caught albacore whose stomachs were examined were between 54 and 117 cm., with 91 percent larger than 85 cm.

4. Stomachs of the larger albacore contained more food than did smaller albacore, but the larger fish ate less per pound of body weight.

TABLE 8.—*Comparison of stomach contents of equatorial albacore (A) and yellowfin (YF) tuna taken on longline more than 25 miles from land during cruise 11 of the* John R. Manning

[(+) denotes organism present, (−) denotes absent. Yellowfin data from files of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu. Sta. denotes station]

Organism	Sta. 8		Sta. 11		Sta. 12		Sta. 14		Sta. 15		Sta. 17		Sta. 19		Sta. 20		Sta. 21		All Stations	
	A	YF	A	YF	A	YF	A	YF	A	YF	A	YF	A	YF	A	YF	A	YF	A	YF
CRUSTACEA																				
Copepoda	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	+	−
Isopoda	−	−	+	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+	+
Amphipoda																				
Phronima sp	+	+	−	−	−	+	−	+	−	−	−	−	−	+	−	−	−	−	+	+
Amphipoda [1]	+	+	+	−	−	+	+	−	−	−	+	−	+	+	−	−	+	−	+	+
Stomatopoda:																				
Squilla sp	−	−	−	−	−	+	−	+	+	−	−	−	−	−	−	−	−	−	+	+
Pseudosquilla sp	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Gonodactylus sp	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
Euphausiacea	−	−	−	−	−	−	+	+	−	−	+	−	+	−	−	−	−	+	+	+
Decapoda:																				
Penaeidae	−	−	−	−	−	+	−	+	−	−	−	+	−	−	−	−	−	−	−	+
Crab megalopa	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+	−	−	−	+
Phyllosoma larvae	−	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+
MOLLUSCA																				
Pteropoda	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+
Octopoda:																				
Argonautidae	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−	−	+
Octopoda [1]	+	+	+	−	−	+	−	+	−	−	−	−	−	+	−	+	−	+	+	+
Decapoda:																				
Loliginidae	+	+	−	+	+	+	+	+	+	−	+	+	+	+	−	+	+	+	+	+
Sepiolidae	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Decapoda [1]	+	−	+	−	−	−	+	+	−	+	−	−	−	+	+	−	−	−	+	+
CHORDATA																				
Tunicata																				
Salpidae	+	+	−	+	−	+	+	−	−	−	+	−	−	+	−	−	−	+	+	+
VERTEBRATA (Pisces)																				
Paralepididae	−	−	−	+	−	+	−	+	−	−	−	−	−	−	−	−	+	−	+	+
Bramidae	−	+	+	−	−	+	−	+	+	−	−	+	−	+	−	−	+	−	+	+
Leiognathidae	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+
Chaetodontidae	−	−	−	+	−	+	−	−	−	−	−	−	−	−	−	+	−	−	−	+
Pomacentridae	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+
Acanthuridae	−	−	−	+	−	+	−	−	−	−	−	+	−	−	−	−	−	−	−	+
Gempylidae	−	−	−	−	+	+	+	−	−	−	+	+	+	+	−	−	+	+	+	+
Thunnidae: *Katsuwonus pelamis*	−	−	−	−	−	−	−	−	+	+	−	+	−	+	−	−	−	−	+	+
Echeneidae	−	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−	−	+
Balistidae	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−	−	−	−	−	+
Monacanthidae	−	−	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−	−	−	+
Ostraciidae	−	−	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−	−	−	+
Tetraodontidae	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	+
Diodontidae	−	−	−	−	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	+
Number of stomachs examined	2	2	1	2	1	5	2	4	2	2	3	3	1	4	1	1	2	4	15	27

[1] Unidentified.

5. The food of albacore was found to consist mainly of a variety of fish, squid, and crustaceans, the percent by volume of each differing according to the method of capture, as shown by the following. Longline: fish, 47 percent; squid, 41 percent; crustaceans, 6 percent. Gill net: fish, 34 percent; squid, 62 percent; crustaceans, 2 percent. Troll: fish, 79 percent; squid, 11 percent; crustaceans, 6 percent. Representatives of 32 fish families and 11 invertebrate orders were found in the food of longlined albacore, compared to 9 fish families and 10 invertebrate orders for troll-caught albacore, and 4 fish families and 5 invertebrate orders for gill net-caught albacore.

6. Fishes of the families Gempylidae and Bramidae dominated in the fish portion of the diet of albacore from the equatorial Pacific, while sauries (Scomberesocidae, *Cololabis* sp.) dominated in albacore caught in the temperate North Pacific. Squid were well represented in the albacore captured by all three methods. The main difference in crustaceans was the lack of stomatopods (Squillidae) in the diet of troll- and gill net-caught albacore.

7. The higher average stomach content of longline-caught albacore (26.7 cc.) was attributed to the larger sizes of these fish. The differences in the average stomach content of approximately the same size gill netted (9.8 cc.) and troll-caught albacore (15.1 cc.) were attributed to differences in the method of capture. Gill netted albacore are taken at night, when feeding is probably at a reduced rate, since 80 percent of the gill netted albacore had stomach contents less than 1 cc.

TABLE 9.—*Comparison of stomach contents of equatorial albacore (A) and bigeye (BE) tuna taken on longline more than 25 miles from land during cruise 11 of the* John R. Manning

[(+) denotes organism present, (−) denotes absent. Bigeye data from files of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu]

Organism	Sta. 16		Sta. 18		Sta. 20		All stations	
	A	BE	A	BE	A	BE	A	BE
CRUSTACEA								
Isopoda	−	+	−	+	−	−	−	+
Amphipoda	+	−	+	−	+	−	+	−
Euphausiacea	−	−	−	+	−	−	−	+
Decapoda:								
Penaeidae	−	−	−	+	−	+	−	+
Homaridae: *Enoplometopus* sp	−	−	+	−	−	−	+	−
MOLLUSCA								
Octopoda	+	−	−	−	−	−	+	−
Decapoda:								
Enoploteuthidae: *Enoploteuthis* sp	−	−	−	+	−	−	−	+
Ommastrephidae	−	+	−	−	−	−	−	+
Decapoda [1]	+	−	+	+	+	−	+	+
VERTEBRATA (Pisces)								
Sternoptychidae	+	−	+	−	+	−	+	−
Paralepididae	−	−	+	+	−	−	+	+
Alepisauridae	−	+	−	+	−	−	−	+
Nemichthyidae	−	−	−	+	−	−	−	+
Myctophidae	+	+	+	−	−	−	+	+
Holocentridae	−	−	−	+	−	−	−	+
Bramidae	−	−	−	+	+	−	+	+
Chlasmodontidae	+	−	−	+	−	−	+	+
Oempylidae	+	−	+	−	+	−	+	−
Tetraodontidae	−	−	−	−	+	−	+	−
Molidae	−	−	−	+	−	−	−	+
Number of stomachs examined	2	1	7	3	6	1	15	5

[1] Unidentified.

8. In the equatorial Pacific, the larger stomach volumes were from albacore captured from latitude 5° S. to 1½° S., whereas the highest catch rates per 100 hooks for albacore occurred south of 5° S. It was concluded that the latitudinal abundance of albacore in the equatorial Pacific, as determined from catch statistics, is not related to the amount of forage consumed by albacore. There was only slight latitudinal variation in the percent occurrence of squid, fish, and crustaceans in the stomachs of equatorial albacore. The amount of squid per stomach was more than twice as much between 5° S. and 5° N. as it was south of 5° S. The lowest amounts of fish and crustaceans per stomach were recorded from 1½° S. to 1½° N.

9. Fishes of the families Gempylidae and Bramidae did not occur in the stomachs of albacore captured by longline in the temperate North Pacific, whereas they were found in 28.5 and 21.5 percent respectively of the stomachs of longline-caught albacore from equatorial waters. It is suggested this may reflect the vertical distribution of these food fishes in these two areas.

10. In the temperate North Pacific, the highest stomach volumes of albacore troll-caught in summer between 140° W.–180°, were found to the south of successive peak volumes of organisms captured by midwater trawling and zooplankton tows. This may show successive trophic levels associated with an advancing oceanographic and biological "frontier" during summer in the Transition Zone of the temperate North Pacific.

11. With respect to longitudinal variations in albacore food in the equatorial Pacific, the highest stomach volumes were recorded in the western portion of the sampling area while the high zooplankton values were recorded in the east central equatorial Pacific. In the temperate North Pacific albacore stomach volumes were higher from 120° W.–140° W. than they were from 140° W.–180°.

12. In the temperate North Pacific, there was little seasonal difference in the volume of albacore food. In the equatorial Pacific the amount of squid and fish varied slightly and irregularly from January through September. From October through December, based on a small sample, the amount of fish consumed was about twice the amount consumed by albacore during other months. In all months more fish than squid was eaten by the equatorial albacore.

13. The amount of squid eaten by equatorial albacore increased with an increase in distance of the place of capture from nearest land. The amount of fish eaten was highest near land (0–24 miles) and then varied irregularly in an offshore direction. Reef-associated organisms appeared most frequently in the diet of albacore captured near land.

14. Feeding by troll-caught albacore in the temperate North Pacific occurred throughout the day. While the lower stomach volumes were found in albacore captured during 1100–1600 hours, the evidence for distinct periods of feeding was not clear. Squid were found in more than 10 percent of albacore stomachs from 0900 to 1700 hours and saurles were common in albacore stomachs (more than 10 percent) throughout the day (0600–2000). Evidence is presented that albacore also feed during the night.

15. The higher stomach volumes of albacore troll caught in the temperate North Pacific occurred in waters of midclarity, as measured by Secchi disc observations.

16. A comparison of the stomach contents of equatorial albacore, yellowfin, and bigeye tunas indicates there may be some competition for food between the albacore and the other two species of tuna.

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APPENDIX

TABLE A1.—*Check list of food organisms found in the stomachs of 348 albacore tuna from the central and northeastern Pacific, 1950–57, according to method of capture*

[Family names of fishes as in Berg (1947) except when indicated. Unid. = Unidentified]

Organism	Longline					Gill net					Troll					All methods combined				
	Number of organisms	Stomachs in which occurred		Aggregate total volume		Number of organisms	Stomachs in which occurred		Aggregate total volume		Number of organisms	Stomachs in which occurred		Aggregate total volume		Number of organisms	Stomachs in which occurred		Aggregate total volume	
		Number	Percent	Cubic centimeters	Percent [1]		Number	Percent	Cubic centimeters	Percent [1]		Number	Percent	Cubic centimeters	Percent [1]		Number	Percent	Cubic centimeters	Percent [1]
COELENTERATA																				
Hydrozoa:																				
Siphonophora *Diphyes* sp.											34	1	1.3	0.7	0.1	34	1	0.3	0.7	
Unid. Siphonophora						20	1	1.1	1.0	0.1	3	3	3.8	0.8	0.1	23	4	1.1	1.8	
ANNELIDA																				
Polychaeta											2	2	2.5	0.3		2	2	0.6	0.3	
ARTHROPODA																				
Crustacea	[1,454]	[116]	[63.7]	[314.5]	[6.5]	[30]	[5]	[5.7]	[10.3]	[1.2]	[585]	[33]	[41.7]	[78.0]	[6.5]	[2,069]	[154]	[44.3]	[402.8]	[5.8]
Copepoda	1	1	0.5	0.4							8	2	2.5	0.1		9	3	0.9	0.5	
Isopoda:																				
Idotheidae	4	1	0.5	0.2												4	1	0.3	0.2	
Unid. Isopoda	23	5	2.7	1.9												23	5	1.4	1.9	
Amphipoda:																				
Hyperiidae	1	1	0.5	1.0												1	1	0.3	1.0	
Lycaeidae											150	1	1.3	6.0	0.5	150	1	0.3	6.0	0.1
Phronimidae:																				
Phronima sp.	75	19	10.4	27.7	0.6	1	1	1.1	0.1		37	6	7.6	13.5	1.1	113	26	7.5	41.3	0.6
P. sedentaria	6	1	0.5	2.0												6	1	0.3	2.0	
Phrosinidae: *Primno* sp.											15	1	1.3	2.6	0.2	15	1	0.3	2.6	
Oxycephalidae: *Oxycephalus* sp.	3	3	1.6	1.0												3	3	0.9	1.0	
Unid. Amphipoda	374	63	34.6	62.4	1.3						72	19	24.0	8.3	0.7	446	82	23.6	70.7	1.0
Stomatopoda:																				
Squillidae:																				
Squilla sp.	119	4	2.2	25.9	0.5											119	4	1.1	25.9	0.4
Pseudosquilla sp.	67	6	3.3	14.5	0.3											67	6	1.7	14.5	0.2
Lysiosquilla sp.	7	3	1.6	4.8	0.1											7	3	0.9	4.8	0.1
Coronida sp.	2	1	0.5	1.0												2	1	0.3	1.0	
Gonodactylus sp.	38	3	1.6	7.6	0.1											38	3	0.9	7.6	0.1
G. guerinii	2	2	1.1	1.7												2	2	0.6	1.7	
Odontodactylus sp.	17	2	1.1	4.0	0.1											17	2	0.6	4.0	0.1
O. hanseni	3	1	0.5	2.0												3	1	0.3	2.0	
Unid. Stomatopoda	288	28	15.4	81.4	1.7											288	28	8.0	81.4	1.2
Euphausiacea	121	14	7.7	9.1	0.2						275	10	12.7	43.6	3.7	396	24	6.9	52.7	0.8
Decapoda:																				
Penaeidae:																				
Gennodus sp.											1	1	1.3	0.1		1	1	0.3	0.1	
Unid. Penaeidae	2	2	1.1	0.7												2	2	0.6	0.7	
Pendalidae: *Heterocarapus* sp.	4	3	1.6	2.8	0.1											4	3	0.9	2.8	
Sergestidae						3	1	1.1	0.5	0.1						3	1	0.3	0.5	
Hoplophoridae	76	2	1.1	14.9	0.3											76	2	0.6	14.9	0.2
Homaridae:																				
Enoplometopus sp.	32	5	2.7	14.0	0.3											32	5	1.4	14.0	0.2
Unid. Homaridae	1	1	0.5	1.0												1	1	0.3	1.0	
Palinuridae	3	2	1.1	2.8	0.1											3	2	0.6	2.8	
Scyllaridae	1	1	0.5	0.5												1	1	0.3	0.5	
Portunidae:																				
Megalops larvae	41	1	0.5	5.5	0.1											41	1	0.3	5.5	0.1
Other crab Megalops larvae	40	8	4.4	9.3	0.2											40	8	2.3	9.3	0.1

See footnotes at end of table.

TABLE A1.—*Check list of food organisms found in the stomachs of 348 albacore tuna from the central and northeastern Pacific, 1950–57, according to method of capture*—Continued

[Family names of fishes as in Berg (1947) except when indicated. Unid. = Unidentified]

Organism	Longline					Gill net					Troll					All methods combined				
	Number of organisms	Stomachs in which occurred		Aggregate total volume		Number of organisms	Stomachs in which occurred		Aggregate total volume		Number of organisms	Stomachs in which occurred		Aggregate total volume		Number of organisms	Stomachs in which occurred		Aggregate total volume	
		Number	Percent	Cubic centimeters	Percent [1]		Number	Percent	Cubic centimeters	Percent [1]		Number	Percent	Cubic centimeters	Percent [1]		Number	Percent	Cubic centimeters	Percent [1]
ARTHROPODA—Con.																				
Crustacea—Con.																				
Decapoda—Con.																				
Phyllosoma larvae	2	1	0.5	0.2												2	1	0.3	0.2	
Unid. Decapoda	92	15	8.2	12.4	0.3						8	2	2.5	1.8	0.2	100	17	4.9	14.2	0.2
Other unidentified Crustacea	9	5	2.7	1.8		26	3	3.4	9.7	1.1	19	10	12.6	2.0	0.2	54	18	5.2	13.5	0.2
MOLLUSCA																				
Gastropoda:																				
Heteropoda:																				
Atlantidae	3	2	1.1	0.2							5	2	2.5	0.4		8	4	1.1	0.6	
Unid. Heteropoda	1	1	0.5	2.2							18	2	2.5	6.4	0.5	19	3	0.9	8.6	0.1
Gastropoda larvae						1	1	1.1	0.1							1	1	0.3	0.1	
Cephalopoda:																				
Octopoda:																				
Octopodidae	18	7	3.8	10.5	0.2						5	2	2.5	3.1	0.3	23	9	2.6	13.6	0.2
Argonautidae	5	4	2.2	17.6	0.4											5	4	1.1	17.6	0.3
Decapoda (squid)	[1,082]	[157]	[86.3]	[1,999.0]	[41.2]	[123]	[25]	[28.7]	[528.3]	[62.1]	[165]	[40]	[50.6]	[131.6]	[11.0]	[1,370]	[222]	[63.8]	[2,658.9]	[38.6]
Loliginidae:																				
Sepioteuthis sp	1	1	0.5	0.5												1	1	0.3	0.5	
Unid. Loliginidae	65	17	9.3	193.7	4.0											65	17	4.9	193.7	2.8
Sepiolidae	1	1	0.5	1.6												1	1	0.3	1.6	
Onychoteuthidae	9	1	0.5	65.0	1.3						1	1	1.3	1.7	0.1	10	2	0.6	66.7	1.0
Enoploteuthidae	26	1	0.5	3.2	0.1											26	1	0.3	3.2	
Ommastrephidae:																				
Symplectoteuthis sp	1	1	0.5	21.0	0.4											1	1	0.3	21.0	0.3
Unid. Ommastrephidae	25	1	0.5	102.5	2.1											25	1	0.3	102.5	1.5
Brachioteuthidae:																				
Brachioteuthis sp						15	1	1.1	89.0	10.5						15	1	0.3	89.0	1.3
Cranchiidae	6	2	1.1	14.5	0.3											6	2	0.6	14.5	0.2
Other Unid. Decapoda	948	138	75.8	1,597.0	32.9	108	24	27.6	439.3	51.6	164	40	50.6	129.9	10.9	1,220	202	58.0	2,166.2	31.4
Other Unid. Cephalopoda	2	2	1.1	6.7	0.1						2	2	2.5	2.4	0.2	4	4	1.1	9.1	0.1
Other Unid. Mollusca											1	1	1.3	0.1		1	1	0.3	0.1	
CHORDATA																				
Tunicata:																				
Thaliacea: Salpidae [2]	104	25	13.7	38.9	0.8						10	1	1.3	8.5	0.7	114	26	7.5	47.4	0.7
Vertebrata (Pisces)	[733]	[152]	[83.5]	[2,282.2]	[47.0]	[30]	[19]	[21.8]	[293.9]	[34.5]	[323]	[45]	[57.0]	[937.5]	[78.6]	[1,086]	[216]	[62.1]	[3,513.6]	[50.9]
Argentinidae											1	1	1.3	1.0	0.1	1	1	0.3	1.0	
Gonostomatidae: [3]																				
Gonostoma sp	2	1	0.5	2.1												2	1	0.3	2.1	
Unid. Gonostomatidae	2	2	1.1	3.0	0.1											2	2	0.6	3.0	
Sternoptychidae:																				
Sternoptyx sp	20	9	4.9	33.7	0.7											20	9	2.6	33.7	0.5
Unid. Sternoptychidae	18	7	3.8	37.6	0.8											18	7	2.0	37.6	0.5
Stomiatidae:																				
Melanostomias sp	3	1	0.5	3.0	0.1											3	1	0.3	3.0	
Unid. Stomiatidae	1	1	0.5	2.0												1	1	0.3	2.0	
Idiacanthidae:																				
Idiacanthus sp											3	1	1.3	0.3		3	1	0.3	0.3	

Synodontidae [4]	1	1	0.5	2.7	0.1											1	1	0.3	2.7	
Paralepididae: [5]																				
Paralepis sp.	4	1	0.5	10.2	0.2											4	1	0.3	10.2	0.1
Unid. Paralepididae	13	6	3.3	34.5	0.7						1	1	1.3	0.8	0.1	14	7	2.0	35.3	0.5
Alepisauridae:																				
Alepisaurus sp.	9	1	0.5	11.0	0.2											9	1	0.3	11.0	0.2
Unid. Alepisauridae	9	4	2.2	23.3	0.5							1	1.3	1.8	0.2	10	5	1.4	25.1	0.4
Myctophidae: [6]																				
Tarletonbeania sp.	26	1	0.5	90.0	1.9						10	1	1.3	16.0	1.3	36	2	0.6	106.0	1.5
Diaphus sp.	1	1	0.5	6.1	0.1											1	1	0.3	6.1	0.1
Unid. Myctophidae	25	6	3.3	23.2	0.5	7	2	2.3	7.5	0.9	17	6	7.6	13.5	1.1	49	14	4.0	44.2	0.6
Scomberesocidae:																				
Cololabis sp.	30	8	4.4	925.0	19.1	11	10	11.5	225.2	26.5	167	20	25.3	733.8	61.5	208	38	10.9	1,884.0	27.3
Cauloleptidae:																				
Anoplogaster sp.	1	1	0.5	1.0												1	1	0.3	1.0	
Unid. Cauloleptidae	2	1	0.5	3.1	0.1											2	1	0.3	3.1	
Holocentridae:																				
Holocentrus sp.	1	1	0.5	1.2												1	1	0.3	1.2	
Unid. Holocentridae	4	3	1.6	3.0	0.1											4	3	0.9	3.0	
Apogonidae	1	1	0.5	1.4												1	1	0.3	1.4	
Scombropidae:																				
Hypoclydonia sp.	5	4	2.2	11.5	0.2											5	4	1.1	11.5	0.2
Unid. Scombropidae	2	1	0.5	1.0												2	1	0.3	1.0	
Carangidae	1	1	0.5	1.5		5	1	1.1	11.0	1.3	40	1	1.3	84.0	7.0	46	3	0.9	96.5	1.4
Bramidae:																				
Collybus drachme	10	9	4.9	36.5	0.8											10	9	2.6	36.5	0.5
Pteraclis sp.	1	1	0.5	6.1	0.1											1	1	0.3	6.1	0.1
Unid. Bramidae	49	22	12.1	83.2	1.7											49	22	6.3	83.2	1.2
Coryphaenidae:																				
Coryphaena hippurus	1	1	0.5	0.7												1	1	0.3	0.7	
Chaetodontidae	6	4	2.2	8.6	0.2											6	4	1.1	8.6	0.1
Champsodontidae	1	1	0.5	0.8												1	1	0.3	0.8	
Chiasmodontidae:																				
Chiasmodon niger	1	1	0.5	2.0												1	1	0.3	2.0	
Unid. Chiasmodontidae	13	5	2.7	21.6	0.4											13	5	1.4	21.6	0.3
Acanthuridae	13	5	2.7	13.1	0.3											13	5	1.4	13.1	0.2
Gempylidae:																				
Gempylus sp.	6	4	2.2	33.0	0.7											6	4	1.1	33.0	0.5
G. serpens	47	18	9.9	140.4	2.9											47	18	5.2	140.4	2.0
Rexea sp.	3	1	0.5	1.6												3	1	0.3	1.6	
Unid. Gempylidae	62	21	11.5	144.0	3.0	1	1	1.1	41.0	4.8	13	2	2.5	6.1	0.5	76	24	6.9	191.1	2.8
Trichiuridae	1	1	0.5	0.1												1	1	0.3	0.1	
Scombridae:																				
Scomber sp.	2	1	0.5	5.0	0.1											2	1	0.3	5.0	0.1
Unid. Scombridae	4	1	0.5	3.8	0.1											4	1	0.3	3.8	0.1
Tetragonuridae: *Tetragonurus cuvieri*	2	1	0.5	3.2	0.1						1	1	1.3	2.0	0.2	3	2	0.6	5.2	0.1
Stromateidae	1	1	0.5	4.6	0.1											1	1	0.3	4.6	0.1
Nomeidae	2	1	0.5	1.0												2	1	0.3	1.0	
Scorpaenidae: *Scorpaena* sp.	4	3	1.6	6.4	0.1											4	3	0.9	6.4	0.1
Thunnidae: *Katsuwonus pelamis*	9	2	1.1	25.1	0.5											9	2	0.6	25.1	0.4
Triacanthidae: *Halimochirurgus* sp.	1	1	0.5	0.3												1	1	0.3	0.3	
Balistidae	1	1	0.5	5.6	0.1											1	1	0.3	5.6	0.1
Ostraciontidae:																				
Lactoria diaphanus	1	1	0.5	6.0	0.1											1	1	0.3	6.0	0.1
L. sp.	1	1	0.5	0.4												1	1	0.3	0.4	
Tetraodontidae	1	1	0.5	0.2												1	1	0.3	0.2	
Molidae	4	2	1.1	0.4							15	2	2.5	2.4	0.2	19	4	1.1	2.8	
Other Unidentified fishes	305	93	51.1	497.4	10.3	6	6	6.9	9.2	1.1	55	21	26.6	75.8	6.4	366	120	34.5	582.4	8.4
Unidentified food and organic residue		12	6.6	180.5	3.7		10	11.5	17.8	2.1		10	12.7	23.6	2.0		32	9.2	221.9	3.2
Total food volume				4,852.3					851.4					1,193.4					6,897.1	
Number of stomachs examined				182					87					79					348	

[1] Given only when 0.1 percent or greater.
[2] The majority were ingested incidentally with the pelagic amphipod *Phronima* sp., which often lives in tests of salps.
[3] Gonostomidae in Berg, 1947.
[4] Synodidae in Berg, 1947.
[5] Sudidae in Berg, 1947.
[6] Scopelidae in Berg, 1947.

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BIBLIOGRAPHY ON THE BIOLOGY OF THE COD, *GADUS MORHUA*, AND RELATED SPECIES

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This bibliography was first assembled as an aid to biological studies of cod (*Gadus morhua*) carried on at the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Mass. It was planned to include only papers on the cod of the northwestern Atlantic, but it soon became apparent that such a compilation would have limited value. Consequently, the bibliography was expanded to include information on the general biology of cod. Papers on *Gadus* species and closely related forms other than *G. morhua* of the Atlantic were included, but no special search was made for them.

Certain criteria were observed in assembling this bibliography, namely: that, with few exceptions, the material be in permanent printed form; that the subject matter be cod biology; that the publication be available to me for reading and abstracting.

A few papers primarily on technology were included because of information contained on basic biological problems, e.g., the chemical composition of the cod or its bacterial flora. Those interested in the literature on technology per se are referred to the excellent bibliography by McPhail, No. 657.

No evaluation of quality or merit for inclusion in the bibliography was made. Articles in print in scholarly journals, books, and more popular works are included. Annotations are usually limited to cross-referencing as an aid in finding related papers. That the material is not all of equal value is partially reflected in the index, where the most important contributions in various biological areas are indicated.

Much has been published about cod, probably for two reasons. First, the cod is one of the world's most important food fishes and its biology and ecology have been widely studied and reported on. Second, it reaches rather large size, is common, and is fairly easy to maintain in captivity because of its tolerance of widely varying temperature and salinity conditions. As a consequence, it has often been utilized by biologists and experimentalists for studies on a "typical" marine fish. As a result, probably more is known of the anatomy and physiology of the cod than of any other marine fish. In addition, physiologists have worked with captive fish in hatcheries both for purely scientific reasons and to learn more about a particular phase of the biology of the cod for the use of fishery scientists. Since a great deal is known about the general biology of these fish, it is much easier to employ cod in studies of a particular phenomenon than to start blindly with an unknown subject.

The bibliography is incomplete in some respects. Specific weakness will be found in the literature published in the Scandinavian and Russian languages. This is partly the result of the unavailability of material, but more particularly to my unfamiliarity with these languages. Fortunately, contemporary Scandinavian workers often publish in English, and many Russian papers carry an English summary or have been translated in part or in full. The lack of completeness is also partly due to the law of diminishing returns. With the attainment of about a thousand references I find it more and more difficult to find those remaining, and there is little hope that they may all ever be found. At the same time, it is probable that most of the more important works have been found and abstracted.

The citations are largely self-explanatory. The name and initials of each author are given as published. Because of inconsistency in spelling and in completeness of names, the work of the same man may appear under slightly varying names. Unfortunately, differing practices in transliteration also contribute to inconsistency of names.

The language of the title is the language of the publication, with the few exceptions, where the authors have furnished English titles. The name, title, and place of publication of a journal are given as they appear in the issue containing the article. The place of publication is not given if explicit in the title.

Coauthors and junior authors are cited with numbers following, referring to the included publications in which they have a part. It was felt that this would serve a useful purpose in grouping organically related work published under the first coauthor's or senior author's names.

Assistance was given by Elizabeth B. Leonard, librarian of the Bureau of Commercial Fisheries Biological Laboratory, by Deborah L. Harlow and staff at the Marine Biological Laboratory Library, both of Woods Hole, Mass.; by other librarians, by my colleagues who called attention to references found in their reading, and by Harriett E. Murray who carefully checked the citations.

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Since completion of this bibliography an important paper has been published on the Pacific cod.

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